



POSTNATAL PHYSICAL AND BEHAVIORAL DEVELOPMENT OF THE JAPANESE WOOD MICE, *APODEMUS* *ARGENTEUS ARGENTEUS*

BY

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ABSTRACT

The morphological and behavioral development and growth of ten captive-born young of four litters of the *Apodemus argenteus argenteus* are described. The young at birth (Day 0) were naked with the eyes closed. The chestnut fur grew on the dorsum on Day 7 and the full juvenile pelage was nearly completed by Day 15. The lower and upper incisors erupted through the gums on Days 9 and 10, respectively, the eyes opened between Days 11 and 13 and the external auditory meatus opened on Day 12.

The newly born young were helpless and inactive. They exhibited a righting response on Day 6 and began to walk on Day 9, and by Day 14 they could walk and jump like the adult, when they are thought to be weaned. The behavioral development was described under the following categories: locomotion and righting, thigmotactic response, grooming, vocalization, sucking, weaning, etc.

The mean weight at birth was 1.3 g and by Day 15 it reached 6.1 g which was almost equal to that of the juvenile trapped in the field.

It was proposed that the developmental process during the pre-weaning period be subdivided into the three subphases: "mother-infant bond establishment phase", "phase of nest-in intention" and "preparatory phase for weaning".

INTRODUCTION

Apodemus argenteus argenteus (TEMMINCK, 1845) is a small terrestrial sylvan rodent with a head-body length ranging from 86 to 100 mm (mean 92.6 mm) and the tail length ranging from 84 to 108 mm (mean 96.2 mm), existing in Honshu, Shikoku, Kyushu and Sado Island, Japan (Imaizumi¹). Data concerning its habitat, home range, breeding habits and population density were reported by Imaizumi², Kanamori³, Miyao et al.⁴ and Kanamori³, respectively. However, no detailed studies on the ontogeny of this subspecies have been undertaken. Knowledge of the ontogenetic pattern of *Apodemus a. argenteus* is essential for a through understanding of

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their species biology. The present paper deals with the postnatal morphological and behavioral development, and growth of the young *Apodemus a. argenteus* born in captivity.

MATERIALS AND METHODS

Of more than 50 specimens of *Apodemus a. argenteus* live-trapped in the Shiga-kogen Plateau (1,600 meters in altitude), Nagano Prefecture, and Aoki-ga-hara (1,000 meters in altitude) at the base of Mt. Fuji, Yamanashi Pref., Central Honshu, Japan, five pregnant females were obtained during the Japan International Biological Program PT section study carried out in 1969 and 1970. Of the five females one failed to suckle her litter. This report is based on the observations on the ten young of the four litters born in captivity to these females. The date of trapping, the date of birth and litter size are shown on Table 1. The females of the *Apodemus a. argenteus* with their litters were confined in aluminum cages each 30×

Table 1. Trapping localities of the females and dates of birth of their litters used in this study

Female number	Locality	Date	Date of birth	Litter size
1	Shiga-kogen Plateau (1,600 meters in altitude), Nagano Pref.	May 29, 1969	June 7, 1969	2
2	Aoki-ga-hara (1,000 meters in altitude) at the base of Mt. Fuji, Yamanashi Pref.	May 16, 1970	May 24, 1970	3
3	Same as No. 1	July 15, 1970	July 25, 1970	3
4	Same as No. 2	Aug. 22, 1970	Aug. 24, 1970	2
5*	Same as No. 1	Aug. 18, 1970	Aug. 24, 1970	5

* This female failed to suckle her litter.

22×13 cm in size with a wooden nest box of 17×12×10 cm. Pieces of paper (2×20 cm each) were provided for the nesting material. The females subdivided them into small pieces and made spherical nests 10 to 14 cm in diameter in the nest box. The animals were fed sufficiently with suitable food (rolled oats, sunflower seeds and commercial dove seeds) and drinking water was supplied *ad libitum*.

Examinations of the young outside of the nest without being anesthetized were made once a day, and the physical development and aspects of behavior were noted. The time spent for the respective observations was no more than a quarter of an hour for fear that the parental care by the females and ordinary normal routine of life of the young would not be disturbed. Because of this limitation of time, certain aspects of behavior,

especially that occurring relatively rarely could not be expected to be observed. Recordings with photograph and movie aided our observations. All animals utilized were deemed healthy and no sex difference was evident in regard to the physical and behavioral aspects of the young *Apodemus a. argenteus*.

RESULTS

I. *Morphological development* (See Fig. 1)

Day 0 (day of birth). The young born was devoid of hair except for the unpigmented mystacial vibrissae growing on the upper lip region. The color of the body was reddish pink, while the digits and the tip of the tail were pale pink. The abdominal viscera and the blood vessels were visible to the naked eye through the translucent skin. The skin of the body was wrinkled vertically. The umbilical scar was prominent. The teats were invisible. The pinnae folded over the region of the future ear openings. The eye slits were not observable and the region of the eye are blackish. The incisors had not erupted through the gums yet.

Day 1. The color of the body turned pink (less reddish than Day 0) and the entire forefoot, hindfoot and tail were pale pink or flesh tint and less translucent. The blood vessels in the region of the head, forefoot, hindfoot and tail presented a good contrast to the light colored skin. A dark pigmentation appeared on the area from the dorsal surface of the frontal region of the head to the inter-scapular region, which became reddish black. The region of the eye was black with a red spot in the center. As Layne⁵⁾ stated, it was the dark iris with a reddish lens of the eye visible through the sealed lids.

Day 2. The dorsal pigmented region became less reddish and darker, especially in the scapular region. The ventral surface became darker. These were in contrast to the light colored lateral part and forefoot. The upper region of the lip where the vibrissae have grown was much swollen and became reddish. Milk in the stomach was hardly visible through the dorsal skin, but apparent through the ventral skin.

Day 3. Pigmentation extended to the upper parts of the base of the tail. The dorsal surface was dark brown and slightly tinged by red except for the flesh tint pinnae. The lightening of the ventral surface of the pectoral and pelvic regions extended to the lateral parts of the dorsal region. The abdominal venter and the upper region of the lip which was red on Day 2 became dark red. The red lens of the eye was invisible and the eye slit appeared as a slight furrow. The pinnae had unfolded, projecting out to the sides of the head. The milk in the stomach was

completely invisible through the dorsal surface but visible through the ventral surface.

Day 4. Pigmentation extended laterally to the pectoral and abdominal sides of the body which was pink on Day 3, and a fairly distinct "plimsol line" marked the lateral limits of the pigmented area of the head and trunk from the pink ventrum. The milk in the stomach was visible through the ventral surface. The pinnae lay flat against the head, almost in contact with the sides of the head, exposing the inner surface outwards. The external auditory meatus remained closed.

Day 5. The dark brown pigment extended half way along the length of the upper surface of the tail tip and the body in general became darker in color. The tail was clearly bi-colored from the base to the middle, while a faint pigmentation extended along the upper surface of the terminal half of the tail. The dark pigmentation also appeared on the ankles of the hindfoot. The pinnae and the ventral surface were flesh tint slightly tinged by black.

Day 6. The dorsal pigmentation became blackish bay. A sparse growth of fine, short and nearly transparent their (measuring up to 2 mm) was macroscopically visible on the area from the lateral part of the pectoral to the lateral part of the pelvic region, if observed carefully. Moreover, the white fur emerged as a fine fuzz through the skin along the dorsal region of the head through the scapular region. In the case of the litter No. 3, black pigmentation of the ankles became enlarged and prominent. The tail was almost bi-colored except for the unpigmented area of the tail tip.

Day 7. The dorsal fur of the head through the scapular area turned to a beautiful golden chestnut color. A white fine fuzz grew on the abdominal and pelvic regions of the dorsum. A black pigment appeared on the upper surface of the carpal region of the forefoot. The pinnae became thick and flesh tint tinged by black.

Day 8. The chestnut fur extended to the entire dorsal surface of the head through the pectoral, abdominal and pelvic regions. As a whole, the dorsal surface of the pectoral region turned chestnut, being influenced by the chestnut-colored long hair while the dorsal surface of the abdominal and pelvic regions looked blackish brown or charcoal grey by a mixture of black pigment of the skin and chestnut color of the hair. White hair grew on the lateral ventrum along the "plimsol line". A sparse growth of white fine hair covered the upper surface of the femur and the forefoot and hindfoot. Milk in the stomach was still visible through the pink skin. The dorsal pigmentation extended along the upper surface of the forelegs to the carpal region, which made the bicolored pattern of the pelage comparable to that of the adult. The pinnae were pigmented dark brown

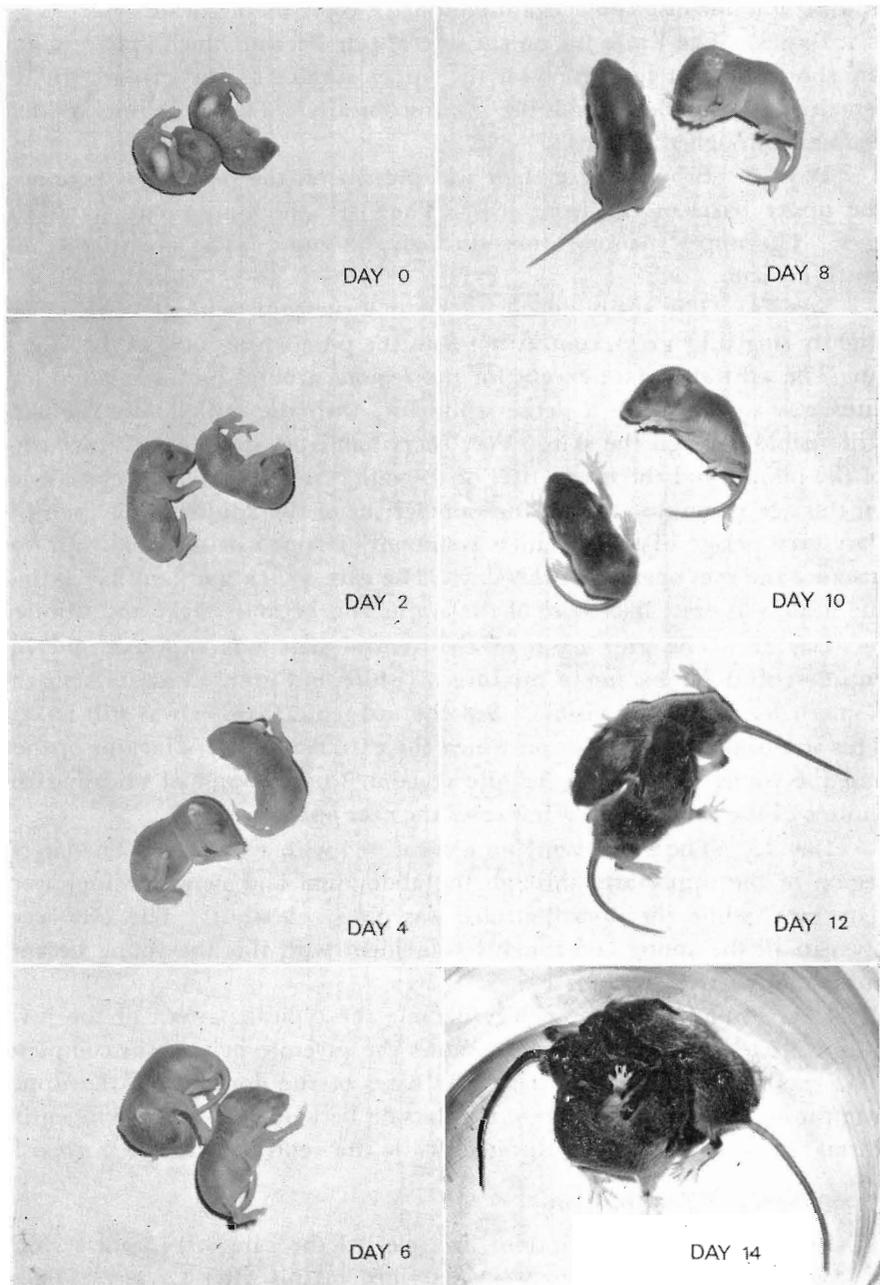


Fig. 1. Series of young *Apodemus a. argenteus* displaying morphological development typical of Day 0 (day of birth) to Day 14 every second day of age.

and became inconspicuous against the dark color of the head.

Day 9. The white fur on the lateral side became much apparent and the short chestnut hair grew on the upper surface of the carpal. In the females the teats became visible macroscopically. The lower incisors had erupted through the gums.

Day 10. Brownish grey hair was present on the pigmented region of the upper parts of the front legs. The dark spots appeared above the eyes. The upper incisors broke through the gums. The eye slit became much evident.

Day 11. The entire dorsal fur became chestnut (with the pelvic area slightly tinged by grey), contrasting with the pure white color of the lateral fur. The ventral surface except for the regions around the uro-genital and anus was covered with a dense white fur, with the milk in the stomach still visible through the skin. Very short hair appeared at the inner edge of the pinnae and the upper part of the tail. As a whole, the pelage color on this age resembled that of the summer fur of the adults rather than the slaty grey pelage of the juveniles commonly trapped in the field. In one instance the eyes opened on this day. The ears, which had lain flat against the head, was erect like those of the adults and became larger and thinner.

Day 12. The grey bases of the ventral hair was exposed, and the entire ventral fur became a mixture of white and grey. The milk in the stomach was no longer visible. But the uro-genital region was still naked. This was commonly the day on which the external auditory meatus opened and the young exhibited a definite reaction to the sound of releasing the shutter of the camera. In a few cases the eyes opened.

Day 13. The whole ventrum was covered with a grey fur. The lateral region of the upper arm through the abdominal and pelvic regions were slaty grey, while the dorsal surface was glossy chestnut. The eyes were open in all the young and roughly coincident with this the young became much more active (Fig. 2).

Days 14 and 15. The pelage became the typical pattern of the juveniles collected in the fields, which shows the juvenile pelage was complete. As a result of exposing the slaty grey bases of the dorsal hair, the upper arm through the pelvic region of the dorsum became darkened. The entire dorsal surface was tinged with olive, while the ventral surface was greyish.

II. *Behavioral development*

In the following descriptions, we selected the categories under which the various types of behavior were described mainly after Layne⁶. These categories have been selected largely as a matter of convenience for descriptive purpose.

1. Locomotion and righting

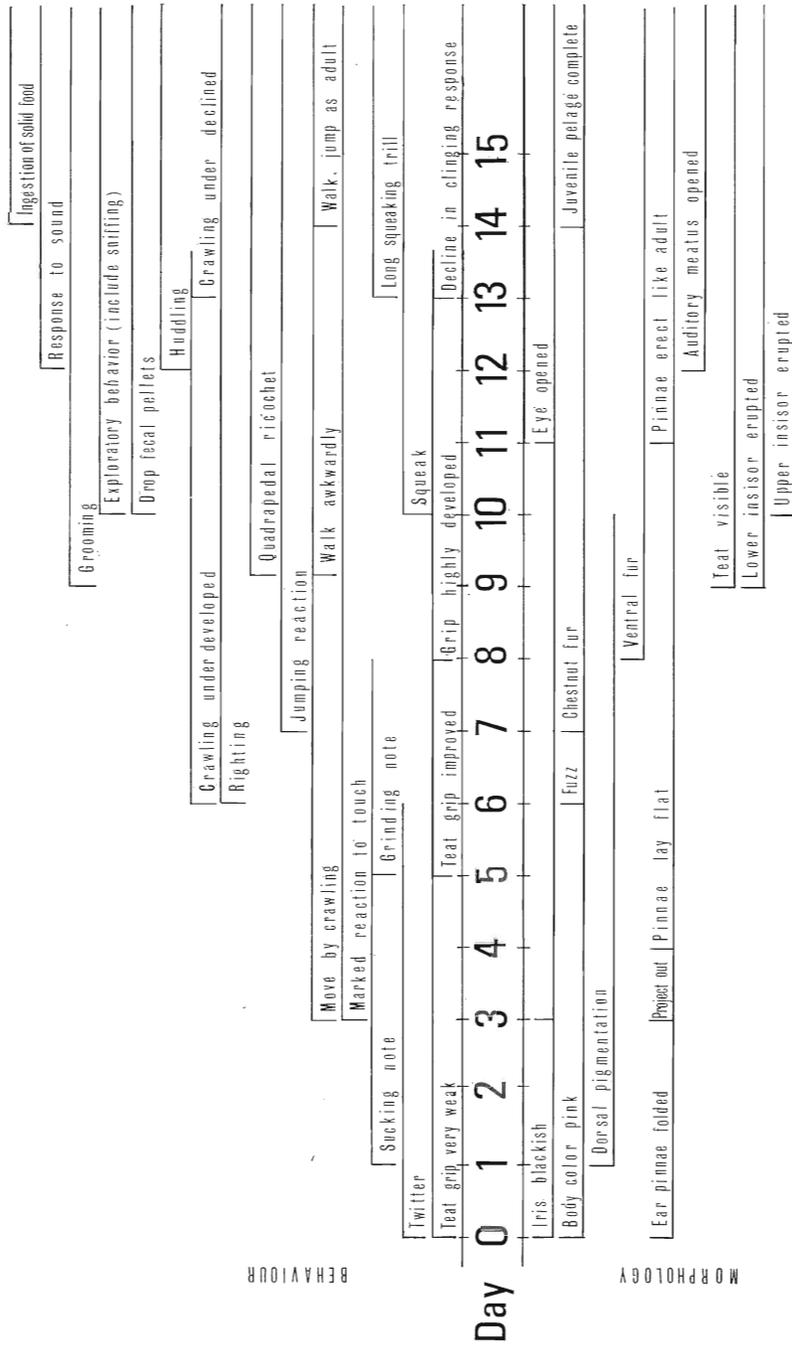


Fig. 2. Chronology of postnatal developmental stages in *Apodemus a. argenteus*.

Day 0 (day of birth). Locomotive ability of the newborn young were poorly developed. The young showed uncoordinated torsal twists and involuntarily rolled weakly from side to side, and was capable of moving a few centimeters from a given spot to an undirected course in an uncoordinated manner. Much of the time the young lay on their sides bending their body and tail ventrally. In this resting posture, the tip of the tail touched the chin and the forelimbs and hindlimbs crossed each other without bending the elbow and knee joints.

Day 1. Same as Day 0 except that they could show attempts to crawl with the forelimbs, but in this manner they were incapable of moving from a given spot. Occasionally the body would twitch spasmodically when inactive.

Day 2. Same as Day 1 except that they made a spasmodic contraction movement of the body when the body was touched.

Days 3 and 4. The young were noticeably stronger. They were seen to lift the front half of the body off the ground by stretching the forelimbs against the ground and could crawl some distance with the forelegs, dragging the venter on the substrate. There was a startle reaction by the spasmodic contraction movement of the body when the body was touched. The young attempted in vain to right themselves. They splayed out their feet when lying on the venter.

Day 5. Same as Day 4 except that the young appeared to be more active and made attempts to escape by crawling when held.

Day 6. Same as Day 5 except that the young resisted being pushed over and attempted to right themselves and eventually did so when rolled over and could crawl backward.

Days 7 and 8. The young generally rested on the venter and exhibited a full developed righting response. They gave a marked jumping reaction when the body was touched.

Days 9, 10 and 11. The young could almost stand and could walk awkwardly for a good distance without tiring, touching the venter on the substrate. When walking, it did rise up on its toes, keeping the heel off the ground as the adult does. Besides, it could also exhibit the quadrupedal ricochet. The young stood upright with its forelegs against the vertical surface.

Days 12 and 13. They could walk faster and more quickly. When walking, the venter was kept apparently off the ground, and the pelvic region was lifted up as compared with the pectoral, which made the walking posture clumsy. The tail was generally kept straight, somewhat off the ground.

Days 14 and 15. They exhibited the same deliberateness in their movements as the adults and a good sense of balance and made use of the

tail in moving about.

2. Thigmotactic responses

The young *Apodemus a. argenteus* displayed with some regularity four types of thigmotactic behavior, besides mutual grooming. These include crawling under, walking over, huddling and nosing.

One young attempted in vain to do crawling under on Day 1. The crawling under tendency was observed not so frequently from Days 3 to 5, markedly increased on Days 6 and 7, and became fully developed on Days 8 through 12. Then, the tendency declined markedly on Days 13 and 14 and was not observed on Day 15. Instead, the tendency of exploration increased.

Walking over was observed several times on Days 10 to 12.

The huddling tendency was recognized from Day 2 and increased markedly from Days 12 to 15.

Nosing (nose to nose contact) was observed only once in the young of litter No. 1 on Day 12.

3. Grooming behavior

The young displayed three basic patterns of grooming behavior. These included scratching with the hindfeet, washing with the forefeet and mutual grooming.

One young was seen to make an abortive attempt at washing (brushing the upper lip with the forefeet) on Day 6. Incipient washing and scratching were noted on Day 9, the former developing fully on Day 12 and the latter became well coordinated on Day 13. Though the general behavior patterns of washing in the young *Apodemus a. argenteus* paralleled those described by Eisenberg⁷⁾ in several species of *Peromyscus*, licking of the genitalia and perineal region during the ventrum wash was not observed. We observed mainly the scratching of the body.

Mutual grooming, that is grooming of one animal by another, was observed only once on Day 12.

4. Vocalization

There were four basic types of sounds produced by the young *Apodemus a. argenteus*. These included a very faint soft twitter which functions in establishing the mother-infant bond, a lower pitched sucking note which occurred when the young were removed from the teats and was accompanied with apparent jaw movements, a faint grinding note which may be produced by the grinding of the teeth, and a louder squeak which may be rather aggressive in its nature and may, under higher intensities of motivation, be emitted as a long squeaking trill.

Imaizumi⁸⁾ recorded a soft twitter vocalization during birth in the *Apodemus a. argenteus*. In our observations of the neonates, this type of vocalization was heard only during the first week after birth (most frequent-

ly on Day 0 and the frequency declined with the increase in age), and was never heard after Day 6. Layne⁶⁾ inclined to think that this type of vocalization functions in establishing a mother-infant bond. Our data obtained here may agree with this hypothesis.

Layne⁶⁾ concluded that once the mother-infant bond is established and the young are less helpless, vocalization diminishes, as any advantages of its continuation beyond the period of maximum usefulness would be counteracted by the determinantal effects of attracting predators to the nest.

Lower pitched sucking note was observed since Days 1 till 5 and it changed to a faint grinding note on Day 6, which lasted till Day 9. Eisenberg⁷⁾ stated that this kind of sound occurs concomitant with the sucking activity and thus is not a true vocalization which results from forced expiration.

On Day 10 the young came to emit a louder squeak and on Day 13 a long squeaking trill was produced as well.

5. Sucking

The young *Apodemus a. argenteus* were usually found on the teats of the mother when she was in the nest during the first two weeks of the post-natal life. The tendency of the young to cling to the teats varies with age. The tenacity with which the young could cling to the teats was very weak and the young dropped off the teats very readily from Days 0 to 4. The grip seemed to be improved on Days 5 to 8 and attempts to pull the young off the mother could result in stretching the teats from the body. From Days 10 to 12, the grip reached its highest development and the young were usually dragged from the nest while clinging to the teats of the mother when she was startled and made a precipitous exit from the nest. The decline in the clinging response was observed from Day 13, and the young were usually found off the teats of the mother from Day 13.

The time when the grip reached its highest development roughly corresponded to the time of the appearance of the incisors (Fig. 2). This kind of phenomenon was already pointed out by Layne⁶⁾ in the *Peromyscus*, who stated that the incisors may aid the young in grasping the nipple. Our data obtained on the *Apodemus* may support his hypothesis.

6. Weaning

Since weaning is a gradual process, it is difficult to define the distinct age of weaning. In general, as Layne⁶⁾ stated in the *Peromyscus* studies, the age of weaning has been estimated on the basis of observations of the young taking solid food, appearance of solid food traces in the feces, or evidence of independence of the young from the mother.

In our observations on the *Apodemus* the young began to take solid food on Day 14. At this age their locomotive ability was almost completed and reached the developmental stage in morphology and weight equivalent

to the juvenile captured in the field, who may go away from the nest of the mother in the field. These data make it possible to consider the age of weaning of the *Apodemus a. argenteus* at about Day 14.

7. Other aspects of behavior

An apparent exploratory behavior was observed from Day 10, which included elongate posture, testing the air and sniffing the substrate.

Fecal pellets were first seen to be dropped during the examination of the young on Day 10. And after this age, the young dropped fecal pellets on each observation day.

III. Growth

Individual weights of the *Apodemus a. argenteus* from birth through Day 16 are given in Table 2. The mean weight of the newborn young is 1.3 g (ranging from 1.1 to 1.4 g), which is 8.8% of the adult mean of 14.8 g (ranging from 10 to 20 g) based on a series of 39 specimens from the Shigakogen Plateau, 1,600 meters in altitude,

Weight exhibited a higher increase rate from Days 5 to 11 than during the first five days following birth. The increase rate declined sharply after Day 12.

The period when the increase rate was high correlated with the time when the grip on the teats of the mother became strong, and the time of decrease in increase rate was roughly coincident with the decline in the clinging response. Moreover, the latter was the time when the eyes and the auditory meatus began to open and the period of weaning.

Following the statement of Layne⁶⁾, the growth and developmental pattern of the *Peromyscus* appear to reflect strongly the differences in the habitat relationship. The neonates of the sylvan species are relatively small to median size, averaging about 8% of the adult weight, and the rates of postnatal growth and development are moderately high. In contrast, the pastoral species exhibit a tendency toward increased neonatal size, averaging about 12% of the adult weight, and a reduction in the litter size to a mean of approximately three. If the theory about these adaptive trends are applicable to the genus *Apodemus*, our data obtained here on the *Apodemus a. argenteus* show that this species belongs to the sylvan species, which is consistent with the sylvan habits of the *Apodemus a. argenteus*.

DISCUSSION

We attempted to analyze the developmental process of the *Apodemus argenteus argenteus* by considering it as the change and development of the individual relationship. The process we have studied in this study forms the pre-weaning phase in the whole life history of the *Apodemus*

Table 2. Daily individual weight of each litter

Age	Litter number	Weight in grams	Age	Litter number	Weight in grams
Day 0	3	1.1	Day 8	1	4.8
	4	1.5, 1.3		2	4.0, 4.2
				4	3.2, 3.7
Day 1	1	1.5	Day 9	1	5.3, 5.4
	2	2.2, 2.2, 2.4		2	4.5
	3	1.3, 1.5		3	3.5, 3.6
	4	1.7		4	3.5, 4.0
Day 2	1	1.9	Day 10	1	5.9
	2	2.2, 2.2, 2.4		2	4.9
	3	1.5, 1.7, 1.8		3	3.6, 4.2
	4	1.6, 1.9		4	3.8, 4.2
Day 3	1	2.3	Day 11	1	6.4
	2	2.5, 2.5, 2.7		2	5.3, 5.5, 5.5
	3	1.7, 2.0		3	4.1, 4.3
	4	1.9, 2.2		4	4.1, 4.4
Day 4	1	2.7	Day 12	1	6.7
	2	2.8, 2.9, 2.9		2	5.5, 5.7, 5.7
	3	2.0, 2.2, 2.3		3	4.0, 4.3, 4.6
	4	2.1, 2.4		4	4.4, 4.5
Day 5	1	3.1, 3.2	Day 13	1	6.8
	2	3.1, 3.2, 3.2		2	5.8, 6.0
	3	2.2, 2.4, 2.5		3	4.3, 4.6, 5.0
	4	2.5, 2.8			
Day 6	1	3.5, 3.6	Day 14	1	6.9, 7.0
	2	3.4, 3.5, 3.5		2	6.3, 6.4
	3	2.3, 2.4, 2.6		3	4.5, 4.7, 5.3
	4	2.7, 3.1		4	5.1, 5.4
Day 7	1	4.1	Day 15	1	7.0
	2	3.9, 3.9		2	6.3, 6.5, 6.6
	3	2.6, 2.8, 3.0		3	5.1
	4	2.9, 3.3		4	5.4, 5.9

a. argenteus. It seems that this phase can be subdivided into three sub-phases from that viewpoint mentioned above.

The first subphase is the first 5 or 6 days (Day 4 or 5) following birth, when the relationship between the mother and infant takes the principal role in the individual relationship; this subphase may be called the "mother-infant bond phase". This subphase is characterized by the behavior of the vocalization of the twitter (Fig. 2). As Layne⁶⁾ pointed out, twitter is thought to function in establishing the mother-infant bond, which therefore enables us to call this also the first subphase "mother-infant bond

establishment phase". In contrast, interaction among the young themselves is scarce.

The second subphase from Days 6 to 9 or 10 is the "phase of infant growth", when crawling under marks the behavior of the young, while twitter became extinct (Fig. 2). Crawling under is the interaction among the young themselves, which is obviously effective in keeping themselves in the nest. On the other hand, the young show no interest about things outside of the nest during this period and we can also call this subphase "phase of nest-in intention".

The third subphase is the period from Day 10 or 11 to 14 or 15. This subphase is characterized by the exploratory behavior and vocalization of aggressive squeak (Fig. 2), both of which show that the young is showing his interest in things outside of the nest. Needless to say, this subphase is a part of the pre-weaning phase and the exploratory behavior is often prevented by the mother. Therefore, we can consider the third subphase "preparatory phase for weaning". This period may be the critical period for establishing the social relationship among the young by exploring each other, though we have no definite data yet.

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