ONTOGENY OF THE LEAST WEASEL (MUSTELA NIVALIS L.)

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This is to certify that the

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Ontogeny of the Least Weasel (Mustela nivalis L.)

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ABSTRACT

Ontogeny of the Least Weasel (Mustela nivalis L.)

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Ontogenetic data were collected on the young of nine litters of least weasels (Mustela nivalis) born in the Michigan State University Museum Live Animal Colony between 10 March 1967 and 13 December 1968. These data included fetal-uterine relationships, litter size, gestation period, neonatal morphology, postnatal morphology, growth, and behavior, and the development of reproductive organs. The information was then compared to that known (from the literature) about the other four North American species of the genus Mustela (M. frenata - long-tailed weasel, M. erminea - short-tailed weasel, M. vison - mink, and M. nigripes - black-footed ferret) in an effort to show the relationships between these closely related species, and to attempt to explain the apparent discrepancy concerning the presence of delayed implantation in the long- and short-tailed weasel and mink and its absence in the least weasel.

Animals were housed in large wooden cages (86.3 x 30.5 x 38.0 cm.) with glass fronts for easy observation. Young animals were observed daily for behavioral changes and weighed and measured at three day intervals. Osteological material was prepared by clearing in KOH and staining in Alizarin Red-S. Histological material was imbedded in paraffin, sectioned at 8-10 μ, and then stained in hemotoxylin and eosin. The uteri of pregnant females were cleared in benzyl-benzoate for study of fetal-uterine relationships.

It was found that in the least weasel two or more litters containing from one to six young are born annually, each after a

gestation period of 35 days. The young weigh about 1.42 grams and measure about 48 mm in length at birth. They have an extremely rapid growth, reaching adult length in about 8 weeks and adult weight between 12 and 15 weeks. In size, males of the American subspecies are larger than females but less so than in the Eurasian forms. Least weasels are weaned and can easily kill mice by 6-7 weeks of age. Female least weasels reach sexual maturity and mate at about four months of age. Spermatogenesis begins at five months of age in the males, however, they do not mate until they are 8 months old.

The litter size of the least weasel does not vary significantly from that of other species of _Mustela_, although the short-tailed weasel tends to have more young per litter. The actual time of implanted development of the long-, and short-tailed weasel and the mink are similar to that of the least weasel, however, their total gestation periods are considerably longer (mink - 40-70 days, long-tailed weasel - 270 days, short-tailed weasel - 300 days) due to the aforementioned presence of delayed implantation in these species. Percentage growth patterns of the least weasel are similar to those of the mink. Most behavioral patterns examined, in which data are available for all species, (_i.e._ killing techniques) show remarkable similarity between the species.

The four major theories for the development and persistence of delayed implantation are reviewed. It is proposed that while the northern geographical range of the least weasel would favor the presence of delayed implantation as in other _Mustela_, the small size and low position of the animal in the food chain would provide a stronger selection against its presence. It was also suggested that, in general, no theory could be used to explain delayed implantation in all the species which exhibit it. Probably during the evolution of the placental system delayed implantation arose independently (as did delayed fertilization) as a method of development and has persisted only in those forms in which it has definite survival value, or possibly serves as a population-limiting factor.

Ontogeny of the Least Weasel (*Mustela nivalis* L.)

By

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INTRODUCTION

The least weasel (Mustela nivalis), in addition to being the smallest member of the family Mustelidae, is also the smallest living carnivore. Its distribution is circumpolar from Norway south to Spain and east across Siberia and into North America (Ellerman and Morrison-Scott, 1966; Hall and Kelson, 1959). The current distribution of the species in North America, based on Hall and Kelson (1959) and extended by the records of Barkalow (1967), Hesket and Fleharty (1965); Jones and Cortner (1965), Jones (1964), Parmalee and Munyer (1966), Schmidt and Lewin (1968), Stupka (1960), Tuttle (1968), and Whitaker and Zimmerman (1965), can be seen in Figure 1.

In addition to the least weasel there are four other members of the genus Mustela in North America: M. nigripes - black-footed ferret, M. frenata - long-tailed weasel, M. erminea - short-tailed weasel, ermine, or stoat, M. vison - mink. Research on these species has centered on three major areas: (a) Economic importance as fur bearers; (b) physiology of delayed implantation; and (c) physiology of coat color change. Because of the close relationships of the members of the genus and the comparative nature of this study it is important to review the literature concerning the ontogeny of each species. Information concerning the least weasel, long-tailed weasel and short-tailed weasel published prior to 1950 has been summarized by Hall (1951).

Least Weasel - Mustela nivalis

The growth and development of the least weasel in North America were almost totally unknown (see Winecoff, 1930; Swanson and Fryklund, 1935; Swenk, 1926; and Polderboer, 1948) until a preliminary report dealing with mating behavior and development of one litter of young born in captivity was published by the author and co-workers (Heidt *et al.*, 1968). However, several studies in Europe have dealt with both the life history and reproductive cycles. East and Lockie (1964, 1965) have observed the growth and development of least weasels born in captivity. Pohl (1910), Goethe (1950), and Muller (1951) have also studied various aspects of the life history. Hartman (1964a, 1964b) reported on mating behavior and life history of introduced animals in New Zealand. The seasonal reproductive cycle of the female weasel has been examined by Deanesly (1944) and that of the male by Hill (1939); however, the ontogeny of reproduction using known-age animals is unknown. From the above studies it has tentatively been concluded that this species does not exhibit delayed implantation.

Long-tailed Weasel - *Mustela frenata*

Life history data on the long-tailed weasel, which is found only in the Western Hemisphere, have been collected by several authors (Hamilton, 1933; Moore, 1945; Quick, 1944; and Sanderson, 1949). The most complete study has been made by Hamilton (*loc. cit.*) in which development, growth, molt, killing techniques, food and miscellaneous behavioral patterns were examined.

Work on the ontogeny of male reproductive organs and the phenomena of delayed implantation exhibited by this species has primarily been done by Wright (1942a, 1942b, 1947, 1948a, 1948b, 1950, 1951). Shelden (1968) has studied histological changes of reproductive organs during gestation and the effect of ovariectomy and ovarian steroid replacement on implantation.

Short-tailed Weasel - *Mustela erminea*

The short-tailed weasel, like the least weasel, is circumpolar in distribution. The most comprehensive work of the life history of the American animal is that of Hamilton (1933) in the same study with the long-tailed weasel. In Europe the growth and development of this species has been the subject of investigations by East and Lockie (1965). Deanesly (1935), Grigoriev (1938), and Muller (1951, 1954). Delayed implantation in this species has been studied in America by Wright (1942a) and Shelden (1968) and in Europe by Deanesly (1935, 1943) Grigoriev (1938), and Watzka (1940).

Mink - *Mustela vison*

Since the mink is economically important, there is a wealth of literature concerning growth curves, litter sizes, nutrition, diseases, genetics, reproduction, and related aspects of the species' biology. Detailed studies of the development, however, appear to be lacking from the literature. Undoubtedly these data abound in the unpublished records of many mink ranchers.

Of the species being considered, studies on mink reproduction are the most common. The overall physiology of reproduction has been studied by Bissonnette (1936), Enders (1939a, 1939b, 1952), and Hansson (1947). The male cycle and maturation of testes has been examined by Bostrom *et al*. (1968) and Onstad (1967). Isolated experiments on factors affecting the delay phase in the cycle have been studied by Aulerich and co-workers (1963), Cochrane and Shackelford (1962), Enders (1961), Franklin (1958), Hammond (1951), Holcomb, Schaible and Ringer (1962), Holcomb (1967), Johansson and Venge (1951), Kirk (1962), Shackelford (1952), and Pearson and Enders(1944).

Black-footed Ferret - Mustela nigripes

This species is among the rarest of North American mammals; however, it appears to be holding its own in some states such as Nebraska (Jones, 1964). The Fish and Wildlife Service (1966) has listed the species as "Endangered and on the verge of extinction". Life history and reproductive data on this species are almost lacking in the literature. Cahalane (1954) reported the finding of 4 young in a nest in South Dakota. Birth of young is apparently in the spring (Jones, 1964), and it is thought that there is no delayed implantation present (P. L. Wright, in litt., 23 April 1969). There are current studies being undertaken in South Dakota to determine the life history of the ferret in the field (Henderson et al., 1968).

Of the five species in North America, delayed implantation has been well documented in three, M. frenata, M. erminea, M. vison, while evidence points against its presence in M. nivalis and the poorly known M. nigripes. One of the goals, therefore of this study is to shed some light on possible reasons for this contrast.

Knowledge of the life history of any species is extremely important, for as Layne (1968) aptly stated, "... knowledge of the ontogenetic patterns .... is essential for a thorough understanding of many other aspects of their biology." The major part of this study is to present data on the ontogeny of the least weasel, covering not only the standard patterns of physical and behavioral changes, but also the maturation of the reproductive structures during growth and, in the case of females, pregnancy. These data will be compared with that known concerning the other four species of the genus in North America, thus providing an up-to-date catalog of known information concerning the ontogeny in these animals.

Figure 1. Current distributional range of the least weasel, *Mustela nivalis* L., in North America.

METHODS AND MATERIALS

Experimental Animals and Maintenance

History of Colony

All weasels, whether born in the laboratory or wild-caught in Sherman live traps, were given a sequence number and toe clipped for permanent identification. This marking consisted of clipping two toes, the first, on one of the fore feet and the second, on one of the hind feet. The toes were clipped in such a way that the animal's identification could be readily detected. In order to avoid possible confusion with other species of mammals in the Michigan State University Museum Live Animal Colony, a 'LW' was placed before the identification number to indicate least weasel. Concurrently with the marking, a data sheet was filled out consisting of the animal's number, sex, location of capture or date of birth, and any other information which could aid in its identification. A complete history was then kept on the weasel and any information pertaining to it was recorded.

The original colony began with two wild-caught weasels, LW-1, a male, caught on the Michigan State University Campus, Ingham County, Michigan on 6 July 1966, and LW-3, a female, caught by hand near the Rose Lake Wildlife Experimental Station, Clinton County, on 17 November 1966. These animals bred and produced an unsuccessful litter on 10 March 1967. They subsequently bred again and a successful litter was born on 28 June 1967. Several more litters were later born to this female and to some of her daughters. In addition, two other animals were caught on the MSU Campus; LW-2, a male, on 7 July 1967 and LW-25, a female, on 30 March 1968.

On 3 June 1968, the colony numbered 26 living individuals, including the four wild-caught animals. On the morning of 4 June all animals were found dead with the exception of LW-24, a female, which had been housed in another room. Four of these dead animals were sent to the MSU Veterinary Pathology Laboratory for autopsy (a summary of the findings can be found in Appendix A).

The remainder of the animals were frozen for later study. These made up the material for the histological and much of the skeletal phase of the study. Four age classes, 3, 5, 9 and 12 months, were present, thus providing a chronological order for studying ontogeny.

On 27 October 1968, a male weasel, LW-32, was captured 1 mile east of the MSU Campus. This animal subsequently bred with LW-24, and a litter of three young was born on 13 December 1968. Two other animals were also caught, LW-31, a female, on 3 October 1968, 2 miles southwest of the MSU Campus, and LW-36, a male, on 15 April 1969, on the MSU Campus. Thus, as of 1 May 1969, the second colony of least weasels numbered 7 individuals (3 males and 4 females). Information obtained from the litter born on 13 December is included here.

Housing and Nutrition

The standard cage in which the weasels were housed consisted of a wooden box having a glass front and measuring 86.3 x 30.5 x 38.0 cm. Entrance to the cage was gained through twin removable tops constructed from 8 mm hardware cloth on wooden frames. After the death of the colony, two additional openings, measuring approximately 15 x 18 cm, were added either in the ends or the back of each cage, to aid in ventilation. The cages were constructed so that a solid or hardware cloth partition could be inserted, dividing the cage in half, thus providing housing for two animals. Single animals were sometimes also housed in standard metal laboratory cages. Wood shavings were provided as bedding for all cages.

This standard wooden cage was used for housing breeding pairs and lactating females, as well as for individuals. When mating between weasels was desired, the cage was divided into two compartments by a 8 mm hardware cloth partition, thereby allowing the male and female to see, smell and hear each other, but not physically associate. The partition was removed for varying lengths of time each day (at no particular time) to allow the animals to associate while under observation. Once the weasels copulated, the male was removed and the female given full run of the cage. Using these methods the exact gestation period could be easily determined, if the female conceived. After the young were born a solid partition was used to exclude the female when the young were examined; thus physically and visually isolating the female.

Two basic types of nest boxes were provided for the weasels. For single animals, a rectangular box measuring 15 x 10 x 10 cm with a 2.54 cm hole drilled in one end was provided. The top was hinged so that it could be opened for cleaning. In the case of pregnant and lactating females a nest box (25.5 x 13 x 20 cm) consisting of two compartments was provided. The top was again hinged for easy observation and/or removal of young. These boxes were open on one side and placed against the glass of the cage, a flap-like cardboard cover was then provided on the glass to cover the rear compartment, allowing further observation with a minimum of disturbance.

The animals were fed a diet consisting of live mice and Purina Mouse Chow. Genera of rodents which were used include: Mus, Peromyscus, Microtus, and young Sigmodon, the majority being Mus and Peromyscus. Water was provided *ad libitum*.

The colony was exposed to photoperiods from incident light, with occasional disruptions by prolonged exposure to laboratory lighting.

For protection of the colony the animals were innoculated with canine distemper and hepatitis vaccine. This treatment consisted of two 0.2 cc subcutaneous shots at a two-week interval.

External Development and Behavior

With the exception of the second litter, which was not disturbed until the fourth day, the young were examined, weighed, and measured on the day of their birth. They were subsequently observed for hair and pigment patterns, tooth eruption, weight gains, increase of body, tail, hind foot, and ear lengths, and other external morphological changes at intervals of three or four days for 4 weeks and then at weekly intervals until they were separated from their mothers at 7 weeks. The young weasels were then weighed at weekly intervals until the age of 15 weeks or until their weight gains ceased. After the age of 4 weeks the young became difficult to handle and were lightly anesthetized with either ether or methoxy fluorine in order to carry out the above observations easily and accurately. The mother was either removed from the cage or separated from the young with a wood partition while the young were examined.

Behavioral patterns were observed at various irregular times throughout the maturation of the young animals. Individual changes were noted and it was attempted to annotate the emergence of a particular pattern and then follow the development of that pattern. Mother-young, young-young, and young-prey interactions were also observed.

The analysis of the ontogeny of vocalization was carried out with the young of litter #3, which was born 6 October 1967. The litter consisted of 6 young (3 males and 3 females). A sequence of vocalizations heard during a particular training phase of another litter (concerning killing of prey) was also recorded. The procedures for recording the vocalizations and subsequent photographing followed that of Huff and Price (1968). Both isolated and group vocalizations were recorded every three to seven days, depending on audible changes in the youngs' sounds, on a Sony 250 tape recorder at 19.0 cm/sec and an Electro-Voice 665C microphone (rated as having a flat response from 40 to 20,000 cps). The recordings were subsequently viewed and photographed on a 502 Tektronix oscilloscope with a 35 mm Grass Oscilloscope camera (showing intersity against time) at f8 and film speed of 50 mm/sec.

Microtechniques

Histological Preparation and Analysis

Immediately after the tissues (ovaries, oviducts, and uteri in the females and testes and epididymides in the males) were removed from each animal they were fixed in either Zenker's or AFA (30 cc 95 percent alcohol, 10 cc commercial formalin, 10 cc glacial acetic acid, 50 cc water) for 24 hours and then stored in 70 percent ethyl alcohol until sectioning was done. The remainder of the carcass was placed in 10 percent formalin and later 70 percent alcohol for further study. Routine dehydration in ethyl alcohol and clearing in xylene was followed by paraffin embedding and sectioning at 8-10 microns. The sections were mounted serially on standard microscope slides and stained with hemotoxylin and eosin.

Dimensions of organs were determined from mounted sections by means of an ocular micrometer mounted in a Swift phase contrast microscope. Photographs were subsequently taken with a Nikon camera mounted on the microscope. Diameters of tubular structures (e.g., oviducts, uterine horns, seminiferous tubules) were taken as the maximum diameter through a "typical" region. In the female structures the muscularis externa was excluded from this diameter because of its considerable variation within any particular uterine horn or oviduct. Volumetric determinations of seminiferous tubules, testes, corpora lutea, and ovaries were computed using the following formula given by Shelden (1968): $V = r_1 r_2 r_3 (4\pi/3)$ where r_1, r_2, and r_3 are the radii of the 3 maximum perpendicular diameters of the gland or organ.

In order to determine better the gross relationship between the embryo and uterus and to attempt to find placental scars in a lactating female the uteri of LW-4 (4 weeks pregnant), LW-15 (11 days pregnant), and LW-3 (lactating) were cleared in benzyl benzoate following the method described by Orsini (1962).

Skeletal Material

The major portion of skeletal material examined in this study consisted of the bacula and skulls (both sexes) of the known-age weasels previously discussed. The skulls were removed from the animals at the same time as reproductive structures. They were subsequently cleaned in the Michigan State Museum dermestid colony and stored in glass vials. Morphological changes in the skull, such as tooth replacement, bone growth and changes in sutures were examined with respect to age and sex of the specimen. Dimensions were taken with dial calipers which measure to 0.1 mm.

In order to examine the morphological changes in the phallus as well as in the bacula, these structures were prepared intact following the method used by Anderson (1960) and others, in which the specimen was first cleared in a 2 percent solution of potassium hydroxide and then stained in Alizarin Red-S stain in a saturated alcoholic solution. After approximately one day the solution containing stain was removed and replaced with 2 percent KOH solution without stain. When the glans became sufficiently cleared that the stained baculum could be easily seen, the solution was replaced by glycerine in which clearing was completed. The baculum was then stored in the glycerine.

Specimens were examined in a shallow dish, containing glycerine, under a binocular microscope. Morphological variations and measurements of the baculum follow those of Long and Frank (1968).

In a previous publication (Heidt et al., 1968) a one-day-old individual was cleared and stained with KOH and Alizarin Red-S as described above, and the ossification of the skeleton was subsequently examined. In order to help clarify this process of ossification, one of the 28-day-old embryos was removed from the uterus, cleared and stained, as described, and the skeletal ossification examined with respect to those centers described for the 1-day-old individual. A 17-day old young was also treated in the above manner.

RESULTS

Ontogeny of Growth and Development

Breeding History

Table I summarizes the breeding history of the weasel colony from January 1967 through December 1968. Reference will be made to this table throughout the remainder of the text.

Fetal-Uterine Relationships

The development of the three species of *Mustela* which exhibit delayed implantation, long- and short-tailed weasel and mink, has been well studied through the blastocyst stage (Wright, 1942a, 1942b, 1948b; Enders, 1939a, 1952; Enders and Pearson, 1946; Hansson, 1947; and Baevsky, 1963). With the exception of the mink (Kissen and Price, 1962) later stages of embryology have not been studied. In an effort to better understand the relationships between the fetus and the uterus in *M. nivalis* the uterine tracts of two pregnant (LW-15, LW-4) and one lactating (LW-3) females were cleared and examined.

Two undifferentiated embryos were found implanted in the uterus of LW-15, which was 11 days post-coitum. This indicates that the developmental time during implantation is around 25 days for the least weasel. This compares favorably with that found in the long-tailed weasel (23-24 days), short-tailed weasel (around 27 days) and mink (28-30 days) (see next section for details). In non-mustelids it has been shown that actual development (from implantation to parturition) is 22-23 days in the laboratory rat (Greenwald, 1967; Enders and Schlafke, 1967). This provides further evidence for the lack of delayed implantation in the least weasel.

Table I

Breeding History of the MSU Museum Least Weasel Colony

Litter Number	Female	Male	Mating Dates	Parturition Date	Gestation Period	Size and Sex of Litter
1	LW-3	LW-1	3 Feb. 1967	10 March 1967	35 days	6 (?) *
2	LW-3	LW-1	22 May 1967	28 June 1967	35 days	4 (2♂, 2♀)
3	LW-3	LW-1	1 Sept. 1967	6 Oct. 1967	35 days	6 (3♂, 3♀)
4	LW-4	LW-2	22 Oct. 1967	26 Nov. 1967	35 days	5 (?) *
5	LW-3	LW-1	12 Dec. 1967	16 Jan. 1968	35 days	6 (3♂, 3♀)
6	LW-4	LW-1	28 Jan. 1968	4 March 1968	36 days	5 (2♂, 3♀)
7	LW-8	LW-6	20 Feb. 1968	26 March 1968	34 days	1 (?) *
8	LW-3	LW-1	11-12 April 1968	18 May 1968	35 or 36 days	6 (3♂, 2♀, 1?)
9	LW-24	LW-32	8 Nov. 1968	13 Dec. 1968	35 days	3 (1♂, 2♀)

* (?) indicates the young were unsexed due to early death.

The uterus of LW-4, which was 28 days post-coitum, contained six embryos, three in each horn. These embryos were well developed, with some skeletal ossification (see section on skeletal ossification for details) and development of major organ systems. It is interesting to note that there was no constant pattern in the orientation of the embryos in the uterus. The vascularization of the zonal placenta always occurred on the medial portion of the uterus, however, the head of the fetus may or may not have been positioned toward the cervical end. In all cases except one the abdominal region of the fetus was located opposite the placenta. In the one exception, the side of the embryo was oriented toward the placenta.

The uterus of LW-3, 17 days post-partum, was examined in an effort to determine the presence or absence of placental scars. The only evidence that this uterus had bore five embryos 17 days earlier, was one, almost indistinguishable, placental scar. This rapid loss of scars would seem to indicate that this method of determining breeding history is at best unreliable, and probably useless. Elder (1952) also was unable to determine the breeding history of mink using placental scars.

Gestation Period

In previous studies on the European least weasel, East and Lockie (1965) were able to record one 35-day gestation period while Hartman (1964a) found gestation lasting from 35-37 days in four pregnancies with European least weasels descended from animals introduced into New Zealand. In this study, as is shown in Table I, the gestation period varied between 34-36 days for the 9 litters. Six of these pregnancies lasted exactly 35 days.

In the long-tailed weasel, Wright (1963) points out that the total gestation period is about 270 days, but the interval between implantation and parturition is only 23-24 days. The gestation period of the short-tailed weasel is about 300 days with the interval between implantation and parturition in the order of 27 days (Wright, 1948a). In mink the gestation period is quite variable (40-76 days), with the embryos implanting 28-30 days before parturition (Enders and Enders, 1963). As previously mentioned, information concerning the black-footed ferret is lacking; however, the gestation period is thought to be in the order of 40-45 days (Wright, *in litt.*, 23 April 1969).

Gestation periods for several of the non-North American species of *Mustela* have also been either shown or estimated:

Mustela putorius (European polecat or domestic ferret) - 41-43 days (Hammond and Marshall, 1930).

Mustela sibiricus (Kolinsky mink) - 28-30 days (Novikov, 1962).

Mustela altaica (Altai weasel) - 40 days (Novikov, 1962).

Mustela eversmanni (Steppe polecat) - 38-40 days (Novikov, 1962).

Mustela lutreola (European mink) - 35-42 days (Novikov, 1962).

Litter Size

Reference to Table I shows that the litter size of nine recorded litters range from 1 to 6, with a mean size of 4.7, which approximates Hall's (1951) reporting of a mean of 5 young for 6 litters found in nature. Among the nine laboratory litters there were 14 males and 15 females, with 13 unsexed due to the early deaths of the young.

In England, East and Lockie (1964, 1965) studied 4 litters of young least weasels born in captivity. These litters ranged from 2 to 7 young with a mean of 5. There were 11 males and 9 females. Hartman (1964a) worked with 4 litters, ranging in size from 3 to 6, with a mean of 4.5. Among these were 11 males and 7 females.

Litter sizes for the five species under consideration are compared in Table 2. Data from the 39 litters produced in 1969 at the MSU Mink Ranch are used for this table and subsequent statistical treatment. It is felt that these figures represent a true estimate of mink litter size, in that Bowness (1968) compared 12,919 litters and found the mean litter size to be 4.77 (as opposed to 4.6 for the MSU mink). Bowness (*loc. cit.*) regarded his figure as slightly high because 40 percent of the mink in the sample were Pastels which had a 4.95 litter average.

Figure 2 shows mean litter size with 95 percent confidence intervals added. From this it can be seen that the only statistical difference between species is that of *M. erminea* and *M. nigripes*.

Condition of Neonate

Least Weasel

At birth the young are wrinkled, pink and devoid of hair. Their eyes and ears are closed and the internal organs, major blood vessels from the head, and sutures in the skull are distinguishable through the transparent skin. The animals are (quite) vociferous, making squeaking sounds (see section on vocalizations), and appear to have fairly good control of their forelimbs but little or no control of their hind limbs. About 6-10 hours after birth the umbilical cord averages about 3 mm in length. The average and extreme measurements (mm) for 8 young were: head and body length, 42 (38-43); tail length, 6 (4-7); hind foot length, 3.7 (3-4); and ear, 0.8 (0.5-1.0). The weight (g.) ranged from 1.09 to 1.70 with a mean of 1.42.

Table 2

Comparison of Litter Sizes of North American Mustela

M. nivalis #/litter	source	M. frenata #/litter	source	M. erminea #/litter	source	M. vison #/litter	source	M. vison #/litter	source	M. nigripes #/litter	source
6	d	8	i	4	c	5	h	6	h	3	g
4						7		1		4	
6		6	f	4	f	4		8		4	
5		7		4		6		2		4	
6				7		2		6		5	
6		2	b	7		2		2		4	
5				8		6		3		4	
1		9	j	9		4		3		4	
6		9				7		7			
3				7	j	7		2			
				5		7		4			
4	m			7		3		7			
4				5		7		9			
						4		1			
5	a					2		7			
						8		4			
10	1					4		4			
3						3		5			
						1		5			
5	k					6					
4											
4	e										
$\bar{X}$ 4.8		$\bar{X}$ 6.8		$\bar{X}$ 6.1		$\bar{X}$ 4.6				$\bar{X}$ 4.0	

a Allen (1940
b Bangs (1896)
c Bishop (1923)
d Current Study
e Dunk (1946)
f Hamilton (1933)
g Henderson et al. (1968)
h MSU Mink Ranch, 1969
i Sanderson (1949)
j Shelden (1968)
k Sutton (1929)
1 Swanson & Fryklund (1935)
m Swenk (1926)

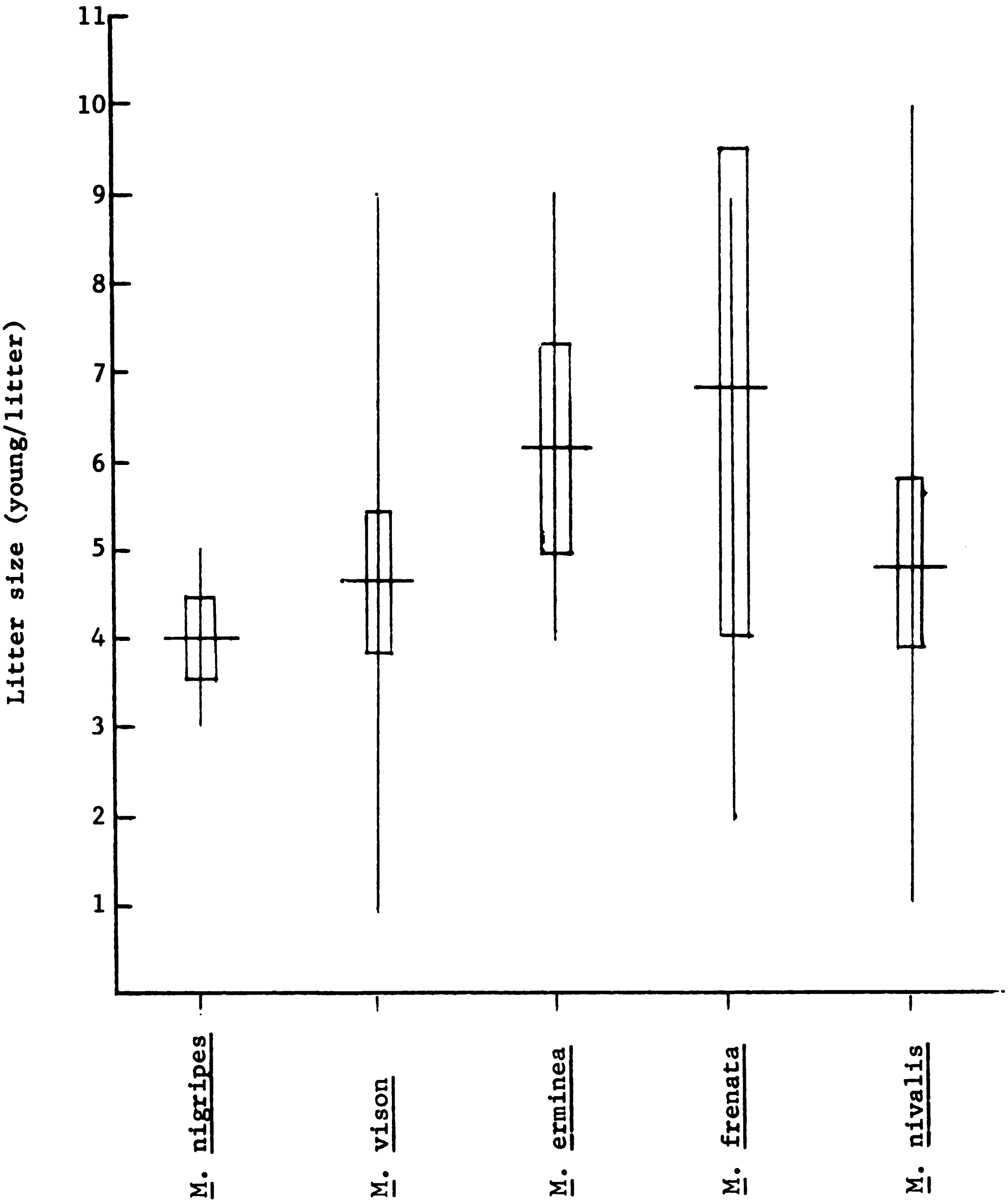


Figure 2. Litter sizes for North American *Mustela*. The vertical line indicates range, the horizontal line indicates mean, and the vertical bar indicates 95 percent confidence intervals ($\bar{X} \pm t_{.05} S_{\bar{X}}$).

Long-tailed Weasel

Hamilton (1933) reports that at birth the young are pink and wrinkled. In contrast to the least weasel he found a few sparse, rather long, white hairs on the back and head. He also pointed out that they have the long neck of the adult, as do all of the weasels.

Short-tailed Weasel

Hamilton (1933) observed that the new born young have a fine growth of white hair on the dorsal surface of the neck, which extends caudad to the shoulder. Short sparse white hairs also appear on the back. The remainder of the body is free of any hair, except the vibrissae. The eyes and ears are unopened.

As in the least weasel the young of this species have better control over the anterior than the posterior portion of their body. Hamilton says, "The young are surprisingly strong. They lift the head high in the air, and support themselves for an instant on their fore legs, but the movements are not coordinated." Like other weasels the young are quite vociferous when disturbed.

The umbilical cords of Hamilton's animals averaged 4 mm in length. The average weight of six new-born young was 1.7 grams.

Mink

No annotated information on the new born mink is available in the literature. However, from observation of preserved young and communication with Dr. Richard Aulerich (of the MSU mink ranch) it would seem that new born mink are fairly typical of the other species discussed.

Travis and Schaible (1961) report that the new born young weigh between 8 and 10 grams.

Black-footed Ferret

No information is available for this species.

Postnatal Development (Morphological)

Least Weasel

Figure 3 shows the developmental sequence for the least weasel. At one day of age the young weasels have fine white hair on the dorsum; by the fourth day, hair completely covers the body. At six days the dorsum begins to show gray pigmentation, which results in a clear demarcation between the dorsal and ventral sides at 10 or 11 days. By 18 days the dorsum is now brown and the ventor white with brownish areas appearing on the thoracic region. The tips of the ears are white. The brown thoracic areas appear to differ with individuals and can be used for individual identifications. Linn and Day (1966) have in fact used this method for identifying weasels in Europe. In most animals these patterns persist until the individual is about 4 months of age and then disappear, leaving the ventor a pure white. As will be discussed later, the disappearance of these areas also seem to roughly correspond with sexual changes and maturity.

The deciduous canines erupt at around 11 days of age, followed in one or two days by all of the incisors. By 18 days deciduous premolars are present. At approximately 30 days the permanent canines can be seen emerging from the gums anterior and slightly lateral to the deciduous ones. The emergence of the permanent canines is well correlated with feeding activities as will be discussed later. The eruption of the

Figure 3. Young of _Mustela nivalis_. (A) One day old young preserved in formalin. (B) Seven day old young. Note covering of fine white hair. (C) Fourteen day old individual. Note grayish-coloring due to dorsal pigmentation.

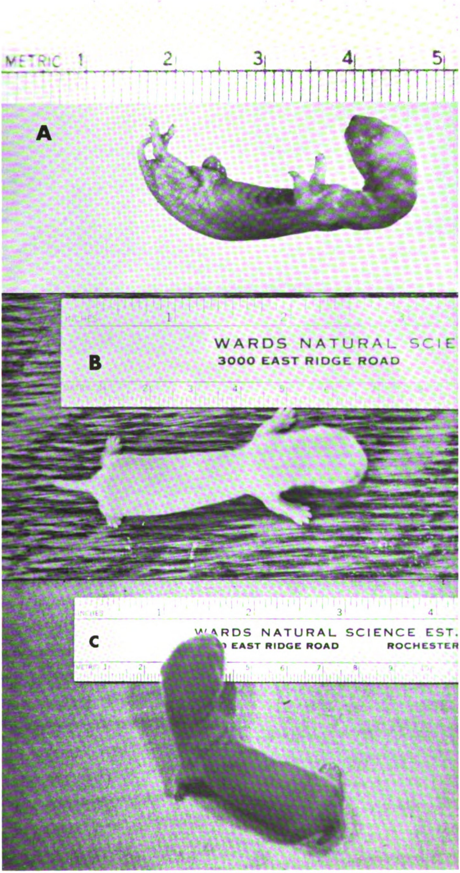
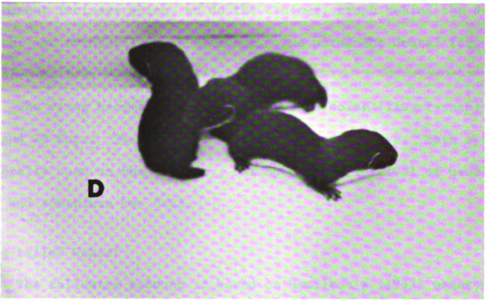
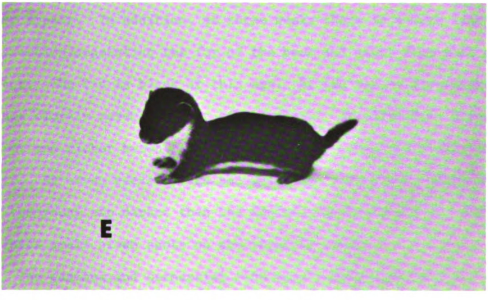

METRIC 1 2 3 4 5
A
B
WARDS NATURAL SCIE
3000 EAST RIDGE ROAD
C
WARDS NATURAL SCIENCE EST.
EAST RIDGE ROAD
ROCHESTER

Figure 3 (cont'd.) (D) 28 day-old young. Note sharp delineation between dorsum and ventor, and white tips of ears. (E) 35 day-old young. Pelage is adult like.


D


E

permanent canines is followed within a few days by the emergence of the permanent incisors which, as do the canines, erupt behind the deciduous teeth, and eventually push them out. The permanent dental formula is: I, 3/3; C, 1/1; P, 3/3; M, 1/2.

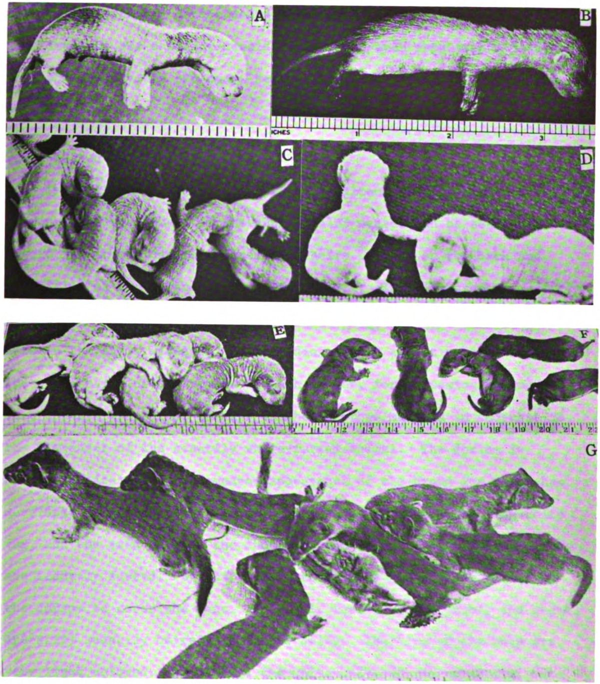
The young become sensitive to a sudden noise (finger-snap) between 21 and 28 days. The eyes open between 26 and 30 days. Both eyes do not generally open on the same day, but open at an interval of usually one day and sometimes two days.

Long-tailed Weasel

The following account is based on Hamilton's (1933) observations. A sequence showing the development of the long-tailed weasel can be seen in Figure 4. At one day the young are covered with fine white hair which is somewhat absent on the legs and belly. This white hair persists until about the age of three weeks when hairs with a grayish color appear. In addition, at three weeks there is a dark line of demarcation separating the fur of the back and sides from that of the ventor. The tip is black at this age. By the age of five weeks the pelage closely resembles that of the adult. It differs in being a darker and richer brown, and the ear margins being noticeably lighter in color. By seven weeks of age the males are darker than the females, and all the young are darker than the adults. Occasionally an individual exhibits small brown spots on the thoracic region.

The canines and carnassial (4th upper) premolars erupt at about 21 days, with the incisors emerging at around 24 days of age. Other cheek teeth also appear at this time. The permanent dentition begins to erupt around 50-55 days and is completed by 75 days.

Figure 4. Young of Mustela frenata. (A) One day old. Note fine covering of white hair. (B) Seven days old. (C) 14 days old. (D) 21 days old. Sexual difference in size can be seen, female on left, male on right. (E) 28 days old. (F) 35 days old. (G) 49 days old. Note relative size of the weasels to that of the adult chipmunk, which weighed 90 grams. (Picture from Hamilton, 1933).

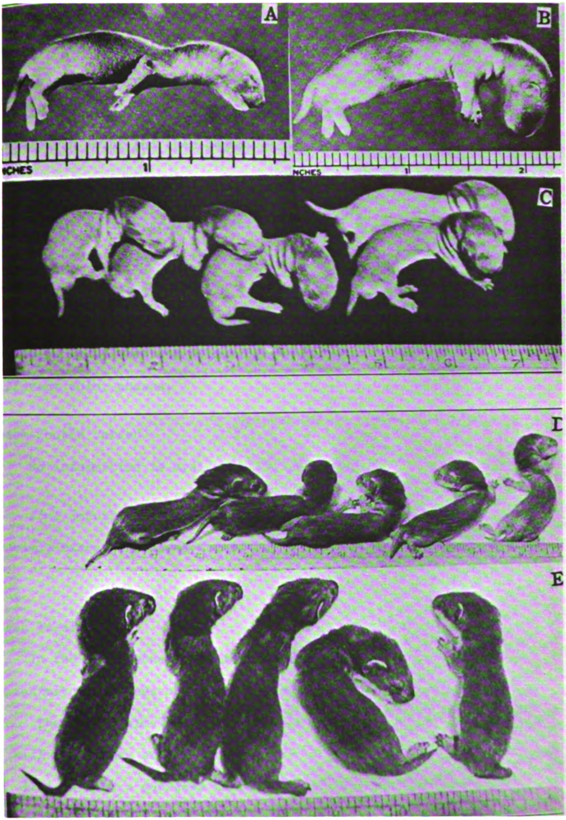

A
B
C
D
E
F
G

No definite information is present on the ability to hear, but the animals can probably detect sound waves by 28 days of age as their vocalizations are changing considerably. The eyes open around 35-37 days and usually one eye opens several hours to half a day before the other.

Short-tailed Weasel

The following account is based on Hamilton (1933). A sequence showing the development of the short-tailed weasel can be seen in Figure 5. At one day there are white hairs present on the back and especially on the dorsal surface of the neck. The vibrissae are quite prominent. At 7 days the animal is darker "... from a line midway between the ears, widening and spreading caudad almost to the shoulders." The white hair in this region is much longer, foreshadowing the mane that appears later. At 14 days the heavy brown mane is in contrast to the remainder of the scantily white-furred animal. The dorsum is darker, indicating the pigmented appearance of the brown fur which has developed by three weeks. The ventor is lightly covered by fine white fur, and the area between the shoulders and facial region and the limbs are scantily furred. By thirty days the fur is almost long enough on the dorsum to cover the mane. The tail, fore and hind limbs, and cheeks are still scantily haired, as is the belly. The tips of the ears are very light colored. By 35 days the white belly fur is appearing, but the inguinal region is still almost bare. The mane is still noticeable. By 45 days the brown fur of the dorsum obscures the mane. The inguinal region is covered by thick white fur, as is the remainder of the belly. East and Lockie (1965) report that in England the black tail tip becomes present at about 45 days of age.

Figure 5. Young of Mustela erminea. (A) One day old. Note presence of fine white hair. (B) Seven days old. Darkened area of the neck foreshadows the mane which appears in a few days. (C) Further prominence of the crest or pompadour. (D) 30 days old. Brown fur of dorsum present. Mane is evident and the black tip of the tail is present. (E) 35 days old. Mane is now fairly well obscured by the rest of the fur on the back. (Picture from Hamilton, 1933).


A
B
C
E

The deciduous canines and carnassial premolars erupt by three weeks of age. The incisors erupt at about 30 days of age. No information is available on the eruption of the permanent dentition.

The ears open at 35 days as do the eyes. When the eyes open they are blue in color and then change to brown in a day of two.

Mink

Again, no annotated information on external morphological development is available from the literature. However, a developmental sequence can be seen in Figure 6. The dentition and tooth replacement (Table 3) has been studied by Aulerich and Swindler (1968a and b). It should be noted that the pelage coloration and changes vary with the different color phases.

Black-footed Ferret

No information is available for this species.

Some important changes during the post-natal development of these species, except the black-footed ferret, have been summarized in Table 3.

Weaning

Least Weasel

In the least weasel weaning is initiated when the young are approximately 32 days old and continues until they are 42-56 days of age. The young animals begin to eat meat around 18 days, but are unable to kill until they are 38-42 days old. Mothers examined when the young are 32 days show a decrease in the size of the nipples, indicating a decline in nursing. After 39 days the mother appears to be easily disturbed by many actions of the young and seems to 'want to get away

Figure 6. Young of _Mustela vison_ through the first three weeks. (Picture from Travis and Schaible, 1961; donated by Dr. R. Aulerich).

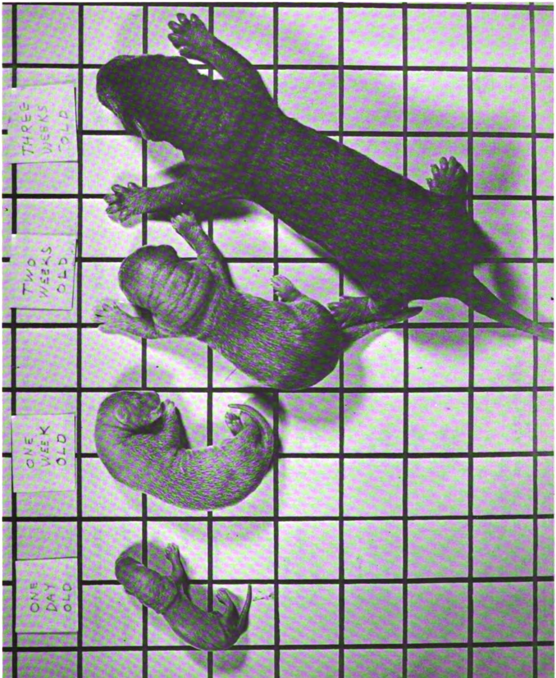

THREE WEEKS OLD
TWO WEEKS OLD
ONE WEEK OLD
ONE DAY OLD

Table 3

Post-natal changes in selected North American members of the genus *Mustela*
Age in days of first appearance

Characteristic	Least Weasel	Long-Tailed Weasel	Short-Tailed Weasel	Mink
Presence of hair	1 day [a]	at birth	at birth [a]	at birth
Dorsal pigmentation	6	21	14	12-16
Brown dorsal fur	18	28-35	21	e
Black tip on tail	none	21	45	none
Thoracic markings	18 [b]	35 [c]	none	?
Mane	none	none	14	none
Deciduous Dentition				
Canines	11	21	21	20-26
Cheek teeth	15-18	21	21	19-27
Incisors	13-14	24	30	16-40
Permanent Dentition				
Canines	30	50-55 [d]	?	53-62
Cheek teeth	35-?	50-55	?	55-67
Incisors	37-45	50-55	?	44-56
Opening of ears	21-28	28?	35	?
Opening of eyes	26-30	35-37	35	?

a - only on dorsum
b - form distinct patterns
c - form only spots in some individuals
d - completed by 72 days in all teeth
e - varies with color phase

from them.' In our laboratory the young are separated at 49 days, and at that time there are occasionally one or two swollen nipples on the mothers, indicating that there may still be some periodic suckling by the young.

Long-tailed Weasel

Hamilton (1933) points out that the young begin eating meat at around 21 days and by 36 days are eating one-half to nearly their own weight each day. He believes they are weaned with the opening of the eyes (28 days). Hall (1951) reports lactation lasting around 35 days.

Short-tailed Weasel

Hamilton (1933) report young begin consuming meat around 21 days of age and by 35 days are consuming more than half their weight in 24 hours.

In Europe, East and Lockie (1965) report that young weasels first killed at the age of 80 days and three of them escaped when 119 days old. The exact period of lactation is not known.

Mink

Travis and Schaible (1961) recommend weaning ranch mink at about 42 days, but keeping the young together from 77 to 112 days.

Black-footed Ferret

Henderson et al. (1968) report that the female ferret begins placing the young, individually or in groups, in different burrows in the beginning of August. If the young are born in May or June, the age at the beginning of the weaning period would be 60-90 days. By late August or early September (90-120 days) the young, now the size of adults, are completely weaned and have dispersed.

Selected Behavioral Development

Locomotion

At birth young least weasels are quite active, having fairly good control of their forelimbs but little or no control of their hindlimbs. By four days of age, the young can stand upright on their forelimbs and crawl by dragging their abdominal region. While quite active at this time they do not move around the nest area. The young can use their hindlimbs effectively by 11 days of age and freely move about the nest area. The young may wander out of the nest for a short distance at this time; however, they are always quickly returned by the mother. At 24 days the young are adept at crawling and can move in a straight line. When the eyes open (28 days), the young become much more active and are often observed leaving the nest for short distances. If there is activity around the cage, the mother will pull them back to the nest; however, if there is no disturbance the young are 'allowed' to remain out. By 30-40 days of age the young have acquired 'typical' mustelid locomotion.

Hamilton (1933) found in long-tailed weasels that there was a difference between the sexes in the development of the ability to crawl. The males could not crawl until they were 14 days of age, at which time they were able to move steadily and in a straight line. The females, on the other hand, were not able to crawl until between 14-21 days. At 21 days both sexes were quite agile. Hamilton (1933) found that short-tailed weasels are quite strong at birth, and can stand on their forelimbs; however, movements are not coordinated. Unfortunately no further observations on locomotion were recorded.

The three species of weasels are primarily terrestrial; however, they are good climbers (Pearce, 1937; Booth, 1945; de Vos, 1960; Jeanne, 1965) and can swim if necessary (Davis, 1942; Green, 1936). The mink is both at home on land or in the water (Burt, 1957) and the black-footed ferret is both terrestrial and fossorial (Hillman, 1968; Henderson *et al.*, 1968).

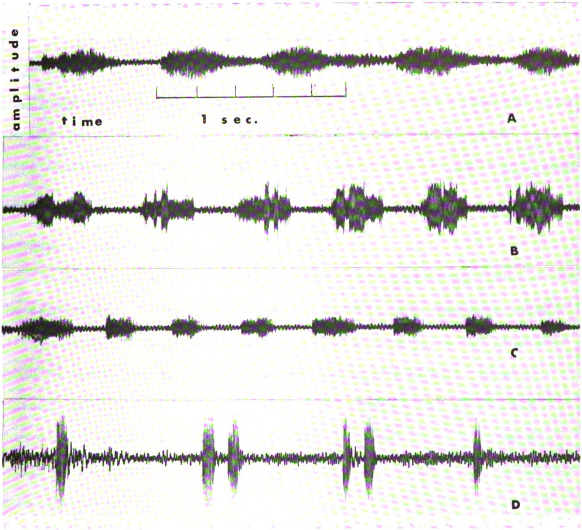
Vocalizations

Vocalizations of adult least weasels have been verbally described by Goethe (1950) and Hartman (1964a). Huff and Price (1968) have analyzed the basic calls with oscilloscope tracings and sonagrams.

Young least weasels are quite vociferous at birth, making high pitched-short bursted squeaking sounds. Figure 7-a shows an oscilloscope tracing of a series of these squeaks taken at 4 days of age. By one week of age these squeaks (Fig. 7-b) appear to be deeper in tone and have developed inflections while being emitted. At 10 days of age (Fig. 7-c) the squeaks have become deeper and sound raspy. This basic pattern continues until the eyes open, or about 28 days of age. There are minor variations, however, such as duration and pitch of the squeak. One interesting variation has the basic squeak with a short hiss-type ending. This hiss resembles that of the adult.

Concurrently with eye-opening the squeak gives way to the chirp (Fig. 7-d). This sound resembles the adult chirp (Huff and Price, *op. cit.*, Fig. 1-a, b) except the ending, immediately following the initial burst, is not as pronounced in the young. Within 2-5 days the chirp is adult-like. Also within 2-3 days after eye-opening the adult hiss is well developed. The trill does not seem to appear until the animal is 35-50 days old.

Figure 7. Vocalizations of young least weasels. (A) Squeaks at 4 days of age. (B) Squeaks at 7 days of age. (C) Squeaks at 10 days of age. (D) Chirp at around 28 days of age.


amplitude
time
1 sec.
A
B
C
D

Hamilton (1933) points out that at 7 days of age young *M. erminea* emit continuous squeaking when disturbed. He describes this note as being similar to the song of a vireo, and audible to a distance of 50 feet. As the young grow older they are rather silent, at least in comparison to *M. frenata*. He describes the squeak of one day old *M. frenata* as being like that of a kitten. He points out that the young are most noisy around 21 days of age, but does not describe the vocalizations. At about 38 days of age they develop the adult *took-took-took* and squeal.

Defense, Avoidance and Aggressive Behavior

It is well known that the mustelids are among the most ferocious of the carnivores. The least weasel is no exception and therefore shows little, if any, avoidance behavior. It does show a defensive behavior which is characterized by set vocal and movement patterns. These patterns seem to be innate and appear concurrently with eye opening. When disturbed or surprised near the nest, the weasel will position itself at the entrance and chirp and hiss (See Huff and Price, 1968, for sound characteristics) at its adversary. Generally half the weasel's body will remain inside the nest area. These vocalizations are accompanied by short thrusts of the head and anterior portion of the body. Often the weasel will retreat into the nest then reappear and go through the same patterns. If bothered to any extent the weasel will emit secretions from the anal glands.

If caught in the open the weasel will stamp the ground with its hind feet and go through the same vocalizations and threat display as described above. In addition the hairs on the tail are erected and the anal scent glands are everted.

If continued to be harrassed the weasel will not hesitate to attack. It seems more prone to attack if not in close proximity to the nest. The least weasel will attack objects much larger than itself, including humans (personal communication, Mr. L. P. Bowdre).

Killing Behavior

The killing behavior of the three weasels has been carefully annotated by several authors (Allen, 1938; Hamilton, 1933; Polderboer, et al., 1941; Glover, 1943; Moore, 1945; and Llewellyn, 1942). The weasel generally grabs its prey at the nape of the neck and then bites through the base of the skull and/or throat area. The weasel uses its feet to manipulate the prey and often wraps its long, slender body around the prey, aiding in leverage.

Actions leading up to killing begin in the least weasel at about 32-38 days of age. Young weasels have shown aggressive behavior towards mice (chirps and thrusts) as early as 32 days of age, with no harm to the mouse. If an immobilized mouse is given to the young during this period (32-38 days) the weasel will play with it, much as would a house cat. At approximately 40 days of age mothers have been observed training the young in killing (see Heidt et al., 1968 for detailed description). By 42-45 days of age the young are quite adept at killing. The ability to kill appears to be an innate phenomena, since young separated from their mother and litter mates before their eyes were open could kill at 50-60 days of age with no previous experience. The training period, therefore, seems to quicken and streamline the killing process, since the un-trained young take longer to become efficient at killing.

Postnatal Growth

Aspects of postnatal growth in North American *Mustela* have been dealt with in several published and unpublished reports. Growth curves of weight and linear measurements for European least weasels have been presented by East and Lockie (1964, 1965) and Hartman (1964), however, since these animals are from 2 to 2 1/2 times larger than North American subspecies, these data will not be used except for comparison with the North American subspecies. Data for *M. frenata* have been partially compiled by Sanderson (1949) and Hamilton (1933). Hamilton (1933) has also presented some data for *M. erminea*. Data for *M. vison* have been reported by Travis and Schaible (1961) and the numerous unpublished records of various mink ranchers. No information is available for *M. nigripes*.

It should be noted that all these data represent laboratory- or ranch-reared animals. Therefore, it is open to question as to what extent the growth patterns of these animals correspond with those in natural populations. In addition, it is important to keep in mind the differences which may result from conditions present in the various laboratories. Ample evidence of the effects of physical and psychological environmental factors on growth in laboratory rodents has been obtained, and these wild carnivores may be even more sensitive to such influences.

Weight

According to Layne (1968: 220) body weight is probably the best single criterion of growth of the whole organism, and knowledge of growth in mammalian species is largely based on this parameter. He also points out that a good advantage of weight as an indicator of overall growth is the relative ease with which it can be obtained as compared with linear or volumetric measurements. One of the disadvantages, at least in small carnivores such as the least weasel, is that the body weight may fluctuate as much as 5-10 grams per day depending on time and amount of feeding. This is a significant percentage when the specimen weighs between 50-70 grams.

Postnatal growth of body weight for the American least weasel is shown in Fig. 8. From these curves it can be seen that the weights of the males and females closely parallel each other until the fourth week when the males gradually begin to add weight. This disparity is not extreme until the eighth week when a further, more pronounced, spurt of growth is shown by the males. A comparison of the American and European least weasel is also shown in Fig. 8. Here it can be seen that the spurt of growth in the European males is at the fourth week of age, and the resulting sexual difference is much more pronounced than in the American form. It also should be emphasized that the overall weight of the European male is 2 to 2 1/2 times that of the American male and the European female is roughly the size of the American male.

Data for weight increases in the long- and short-tailed weasels are too scattered and scanty in the literature to make any valid comparisons. Fig. 9 shows the growth curves for ranch-raised mink as compiled by Travis and Schaible (1961). These curves are very similar to the least weasel in that the males and females parallel each other to the 4th week, and the males' growth begins to spurt around the eighth week.

Table 4 compares the growth rates of the least weasel and mink in terms of adult weight. Age at half-growth estimated from Figures 9 and 10 is also included in the Table. It can be seen that the most rapid

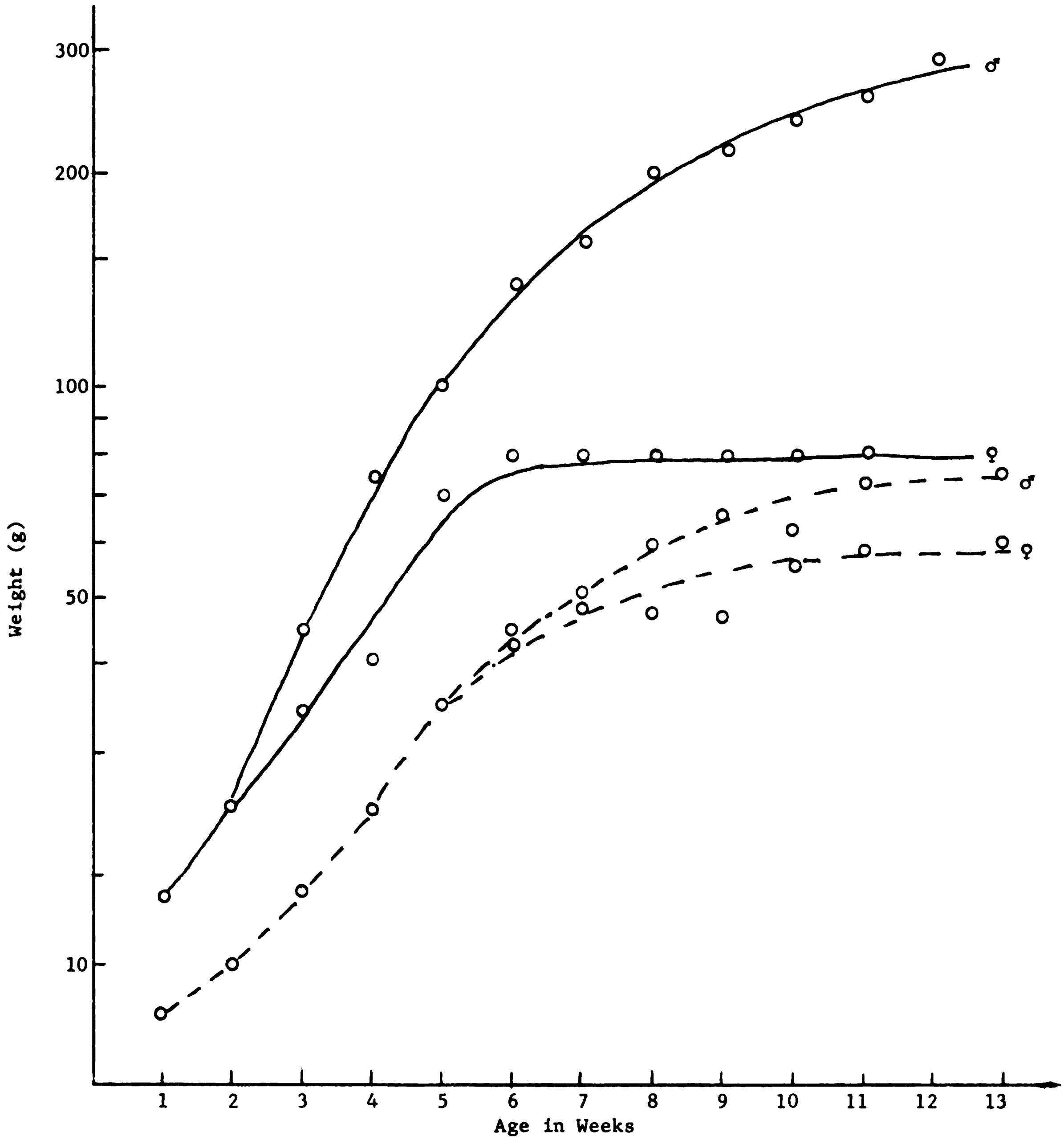


Figure 8. Semilogarithmic plot of growth in weight of the European (solid line) and American (dashed line) least weasels. Data for European least weasels from East & Lockie (1964).

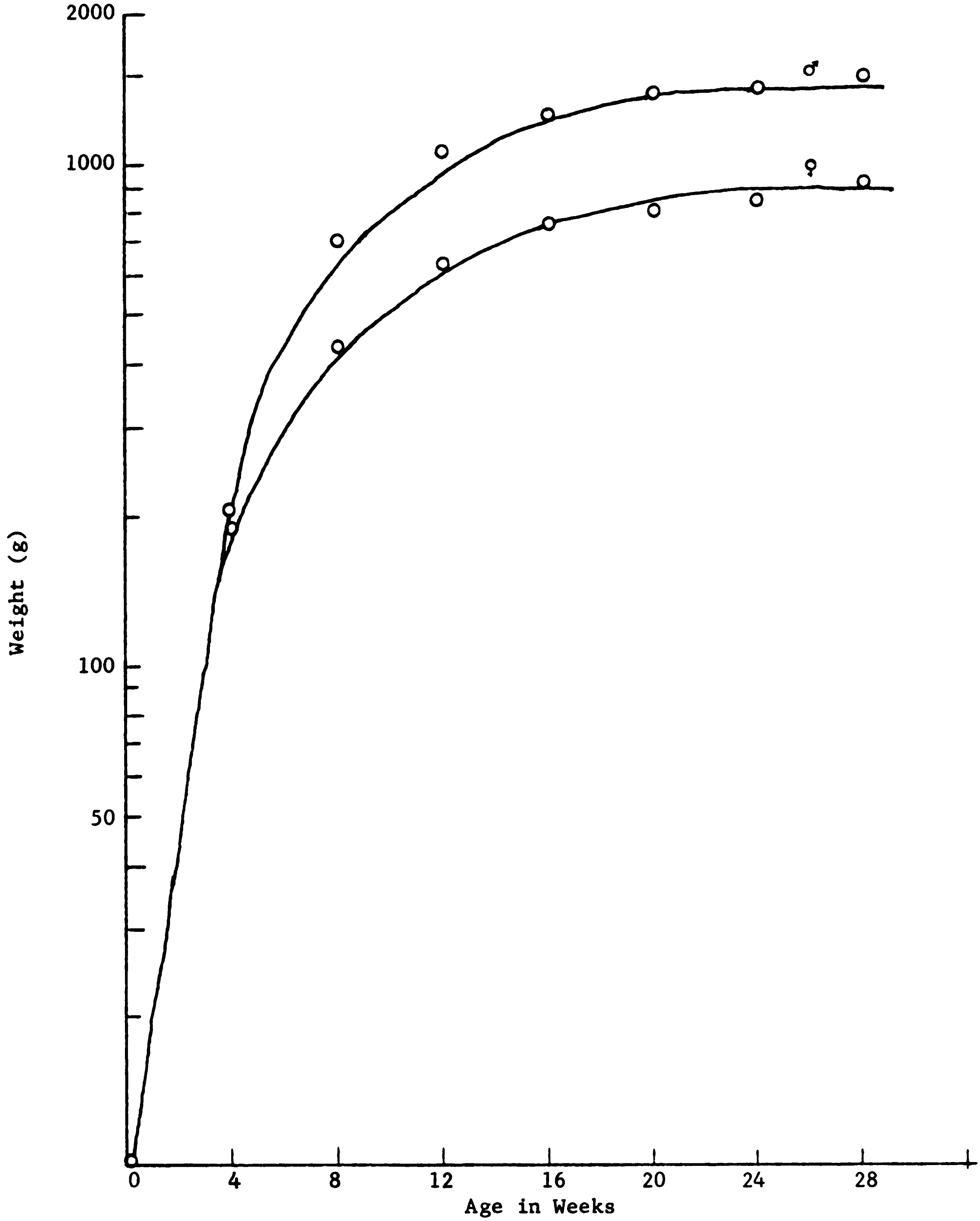


Figure 9. Semilogarithmic plot of growth in weight of the mink. From Travis & Schaible (1961).

Table 4

Postnatal Growth in Weight Expressed as a Percentage of Mature Weight and Approximate Age at One-Half Growth in *M. nivalis* and *M. vison*

Species	Age in Weeks 1	2	3	4	5	6	7	8	9	10	11	12
M. nivalis												
♂	6.9	13.5	22.9	42.4	56.3	59.3	66.9	79.9	88.8	----	97.22	----
♀	8.8	16.3	29.0	51.6	56.3	71.9	80.2	79.0	----	92.2	100.00	----
M. vison												
♂		5.9		11.8		22.1		39.7		62.9		69.1
♀		10.0		20.0		32.5		50.0		67.5		74.5

Species	Age in Weeks (Continued) 13	14	15	16	17	18	19	20	21	22	23	24	One-half growth, days
M. nivalis													
♂	100	----	----	----	----	----	----	----	----	----	----	----	33
♀	---	----	----	----	----	----	----	----	----	----	----	----	27
M. vison													
♂		73.5		80.9		88.2		94.1		98.5		100	63
♀		80.0		97.5		92.5		97.5		100.0		---	56

period of growth in the female least weasel is between the third and fifth weeks, thus lagging approximately one week. In the mink the most rapid period of growth is between the sixth and tenth weeks in both sexes. It is interesting to note that the half-growth of the males of both species is about two weeks later than that of the females.

If the rapid growth periods are calculated as a percentage of the total period of growth, the figures are 16.4-30.8 percent for the female least weasel as compared with 27.3-45.5 percent for the female mink. The figures are 23.1-38.5 percent for the male least weasel as compared with 26.0-37.5 percent in the male mink. The half-growth falls at 29.7 percent in the female least weasel as opposed to 25.5 percent in the female mink. Interestingly, the male least weasel is 36.3 percent and the male mink 37.5 percent. Thus, when the rapid period of growth for the two species is compared in this way the growth patterns for the males of both species are close, indicating a basic similarity. The female least weasel seems to begin and end this period earlier than does the female mink.

Body Measurements

Growth curves of head and body, tail, hind foot, and ear in the least weasel are shown in Figures 10 and 11. Growth data for body dimensions are also presented as percentages of adult size in Tables 5-8. No data for these measurements in the other species of Mustela have been found in the literature.

All four of the body measurements considered reach mature size more rapidly than the body weight. This may be due in part to the fact that weights of neonatal least weasels are about 2 percent of the adult whereas body measurements range from 18-27 percent of corresponding adult values.

All measurements have reached the adult size at 49-56 days, however, the hind foot appears to approach this size the most rapidly; half-growth being attained at 16-17 days. Head and body length appears to follow the hind foot in speed (half-growth 15-19 days), with ear and tail following, growing at similar rates.

Both males and females grow evenly until one week of age when the males appear to lag behind almost exactly one week (Table 5). This apparent lag, however, may be due to the fact that the male is larger when adult size is attained (note that both sexes have attained adult size at 8 weeks). Application of the non-parametric Wilcoxon test shows no significant differences between the sexes. This is surprising when the sexual dimorphism in overall size is very striking in the European least weasel, as well as the other mustelids.

Skeletal Growth

Ossification

Three specimens (a 28-day embryo, a 1-day neonate, and a 17-day young) were cleared and stained in an effort to discern ossification during skeletal growth. The lower jaw, except for the anterior-most portion, of the 28-day embryo, crown-rump 13 mm (Fig. 12), was well ossified. The lateral and ventral aspects of the skull showed ossification to the point that most individual bones could be discerned. The bones, while thin and fragile, varied in thickness and had a lattice-like appearance. No ossification was present on the dorsal aspect. On each side the zygomatic process was about 2/3 complete, the incomplete coronoid process of the lower jaw rested on the inner surface of the incomplete zygoma. The occipital bones were identifiable but separate with little ossification. Portions of the ventral aspect of

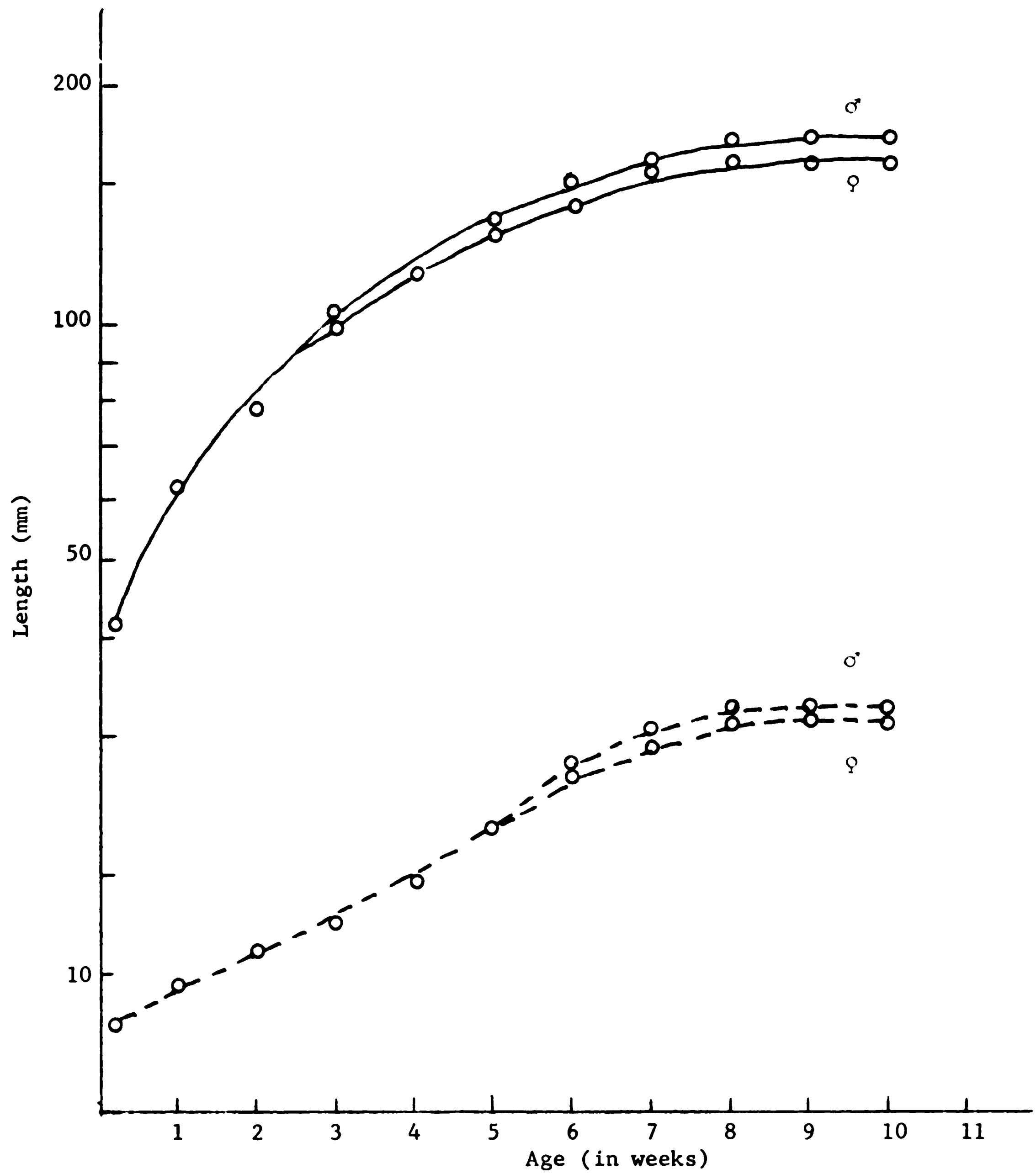


Figure 10. Semilogarithmic plot of growth in the head and body length (solid line) and tail length (dashed line) in the least weasel.

Table 5

Postnatal Growth in Head and Body Expressed as a Percentage of Mature Length and Approximate Age at One-half Growth in *M. nivalis*

		Age in Weeks								One-Half Growth-days
Sex	Day 1	1	2	3	4	5	6	7	8	
♂	24.0	36.1	45.2	58.4	66.8	77.4	86.5	93.5	100	19
♀	26.2	39.6	59.5	63.8	73.3	85.5	93.7	99.1	100	15

Table 6

Postnatal Growth in Tail Expressed as a Percentage of Mature Length and Approximate Age at One-Half Growth in *M. nivalis*

		Age in Weeks								One-Half Growth-days
Sex	Day 1	1	2	3	4	5	6	7	8	
♂	18.9	27.1	33.3	56.2	59.1	71.6	84.0	92.8	100	24
♀	18.8	27.8	34.2	55.8	59.6	72.2	86.4	95.1	100	24

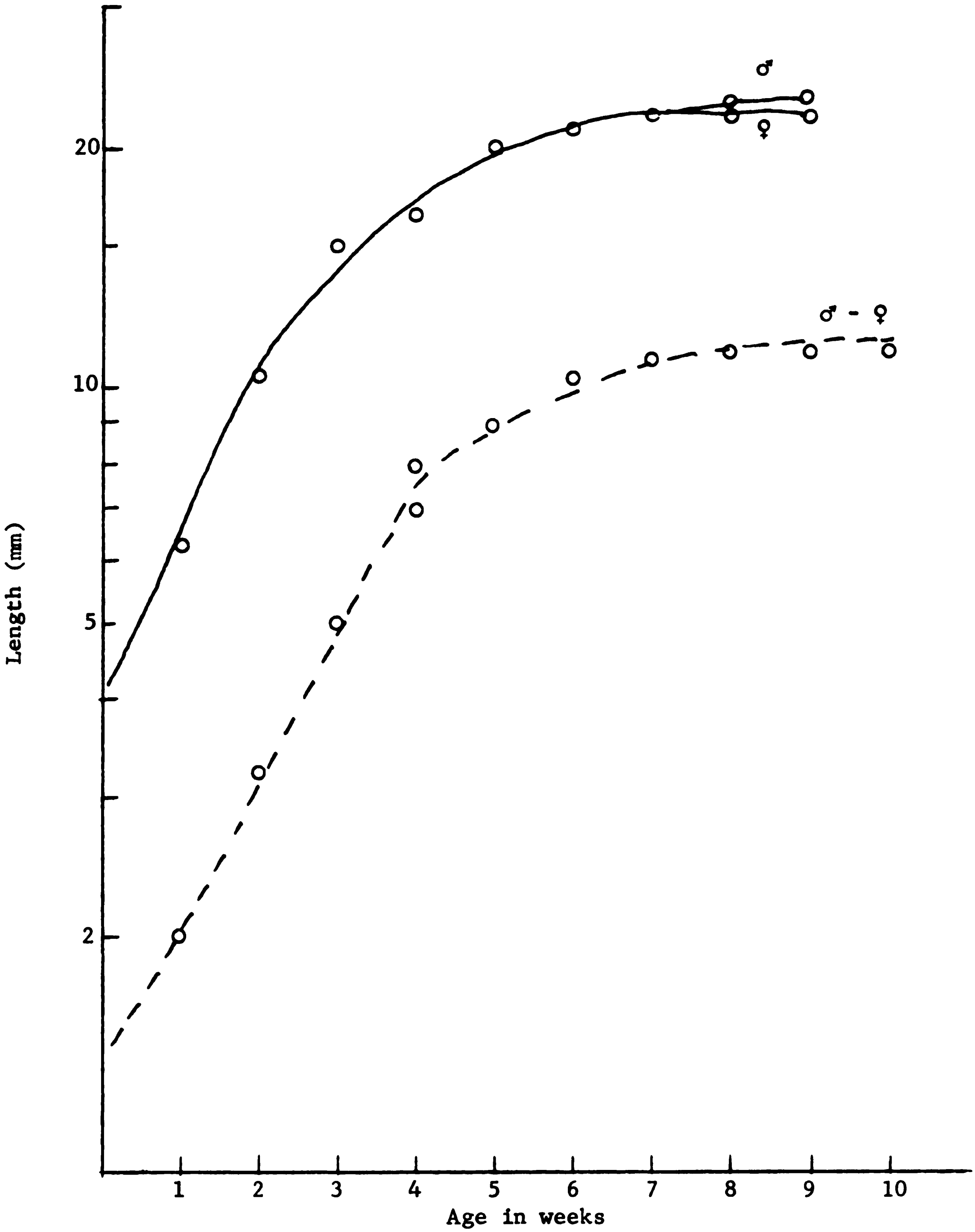


Figure 11. Semilogarithmic plot of hindfoot (solid line) and ear growth (dashed line) in the least weasel.

Table 7

Postnatal Growth in Hind Foot Expressed as a Percentage of Mature Length and Approximate Age at One-half Growth in *M. nivalis*

Sex	Age in Weeks 1	2	3	4	5	6	7	8	One-Half Growth-Days
♂	27.8	47.0	66.5	73.9	86.9	91.3	95.7	100	17
♀	29.5	48.6	66.4	77.3	90.0	95.4	100.0		16

Table 8

Postnatal Growth in Ear Expressed as a Percentage of Mature Height and Approximate Age at One-half Growth in *M. nivalis*

Sex	Age in Weeks 1	2	3	4	5	6	7	8	One-Half Growth-Days
♂	16.7	29.2	51.7	68.3	77.5	89.2	94.2	100	24
♀	17.5	30.7	53.9	69.3	77.2	93.0	100.0		22

the skull were ossified, but poorly developed with little fusion. Tympanic bones were present, but only the dorsal-most portion showed any ossification. No ossification was present in the presphenoid and vomer, and the basispenoid was separated by a gap of 0.5 mm. The palatines were not fused. The orbits were formed but not well ossified. None of the teeth were apparent.

Of the vertebrae only the atlas and axis were ossified, however the centrum of 12 others (remaining five cervical and 7 thoracic) showed evidence of ossification. The remaining parts of these vertebrae, as well as the others, could be discerned but were not ossified. Thirteen pairs of ribs were present; none showed any deposition of bone in the sternal portions. No sternal elements were present.

None of the bones of the pelvic girdle was present. In the pectoral region part of the scapula was ossified. The hind limbs appeared to be not as well developed as the forelimbs. None of the leg bones, consisting of tiny osseous cylinders, was complete; no adult processes and projections had formed. No tarsal or carpal elements were present.

By one day of age (Fig. 13), the skull and lower jaw were well ossified, but still varying in thickness and lattice-like in appearance. Individual bones on the dorsal aspect of the skull were readily discernable. On each side the zygomatic process was complete, and the coronoid process of the lower jaw rested on the inner surface of the zygoma. The occipital bones, while now well ossified, were still separate. The ventral aspect of the skull remained poorly developed with little fusion. The dorsal half of the tympanic bones were now ossified, giving the appearance of a cup-shaped structure. There was still no ossification of the presphenoid and vomer, and the basisphenoid was still separated from the basioccipital. At this age the palatines were fused along the posterior four-fifths of the hard palate, but the ossified areas of the palatine portions of the maxillary were separated by a narrow space. The orbits were now well ossified but delicate. The pterygoid had developed to the point that hamular processes were evident.

The cusps of several cheekteeth as well as canines and incisors, all deciduous, were now emerged from the alveoli in the upper and lower jaws, giving the following dental formula: I, 2/2; C, 1/1; P, 1/2; M, 0/0. The permanent dental formula, as previously mentioned, in the adult weasel is: I, 3/3; C, 1/1; P, 3/3; M, 1/2.

A total of 40 vertebrae (7 cervicals, 14 thoracics, 6 lumbars, 3 sacrals, and 10 caudals) were ossified. This number is the same as in the adult except for the caudals, which total 14 in skeletons of four adults examined from the MSU Museum collection. Hall (1951) stated that the caudal vertebrae number 11 to 16. The apparent disparity in the number of caudals is due to the fact that the terminal vertebrae were in an unossified condition, and thus were not counted. All vertebrae, except the distal seven caudals, were composed of three separate elements, the centrum and two dorsal arches. The distal seven caudals consisted of centra only. Fourteen pairs of ribs were present, although still none had any deposition of bone in the sternal portions. Eight sternal elements were present, with the first and eighth about a fifth as large as the others.

In the pelvic girdle only the ilium and ischium were present. The ilium was an elongated piece of bone (length 1.15 mm), whereas the ischium (length 0.6 mm) was triangular. These bones were 1.27 mm apart. The hind limbs appeared to be not as well developed as the forelimbs; as previously noted the day-old animal could use its forelimbs more efficiently than it could its hind limbs. The leg bones, still consisting of tiny osseous cylinders, had not yet developed any of the adult processes and projections. No tarsal or carpal elements were present.

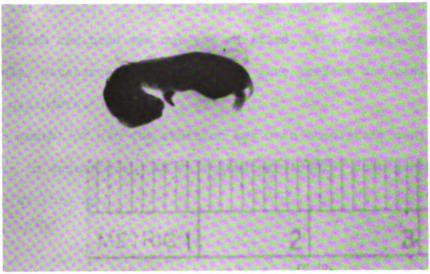
By 17 days the skull and lower jaw of the young least weasel were well ossified, however, the sutures were fragile and when the skull was cleaned the bones separated from each other. The dental formula (all deciduous teeth) at this age was: I, 3/3; C, 1/1; P, 3/3; M, 0/0. The processes and spines of the cervical, thoracic, and lumbar vertebrae were present and well formed, however, the individual components of the vertebrae were easily distinguished from each other. The first five caudals showed the beginnings of the neural spines, however, they were distinctly separated from the centra. The remainder of the caudals (7) were small osseous cylinders well separated from one another.

Fifteen pairs of ribs were present. These were adult-like in appearance with cartilaginous connections to the sternum. Eight sternal elements were present, however, ossification was not complete. The portion of the manubrium, anterior to the first thoracic rib, while present, had not begun to ossify. The remainder of the bones were about 2/3 ossified, with the bony portion occupying the central part of the element.

The pectoral girdle was present and well ossified. The spines and processes of the scapula were well formed. In the pelvic girdle the three bones were present, but not completely ossified. The ilium and

Figure 12. Twenty-eight day old embryo cleared and stained to show skeletal ossification.

Figure 13. One day old young cleared and stained to show skeletal ossification.


METRIC 1
2
3


METRIC 1
2
3
4

ischium were almost completely formed, but had not yet fused. The body of the pubis was ossified, but the ramus was not formed and there was no fusion with the other two pelvic bones. The long bones of the legs were ossified and had most of the processes, the notable exception was the femur in which the head was not yet ossified. The carpals, tarsals, metacarpals, metatarsals, and phalanges were present and consisted of ossified cylinders.

By 3 months of age the skeleton has been completely ossified and is adult-like in appearance. As indicated previously, body growth is completed by this age.

Skull

Table 9 shows measurements for the skulls of least weasels, comprising 2, 3, 5, 8, and 12+ month age intervals. These measurements, with the exception of sagittal crest height, follow Hall (1951). Changes between these age groups can be seen in Figures 14 and 15. As can be seen from the table, the skull, except for the sagittal crest, has completed growth, in both sexes, by the third month of age. In addition, while the male skull is slightly larger in most cases, there appears to be no significant difference between the sexes (again excepting sagittal crest). Since sagittal crest height appears to differ according to both age and sex, 95 percent confidence intervals have been shown in Figure 16. As can be seen there appears to be a significant difference in the males between the five and 8 month age group, and a difference between the females and the 8-12+ month group of males. In the weasel, the adult male's head is noticeably broader than the female's. This difference can be partially explained by the higher sagittal crest in the male allowing for greater muscle attachment.

With the exception of a diagram showing changes in the skull of the long-tailed weasel (Hamilton, 1933) no information concerning growth in known-age skulls is available for the other 4 species.

Table 9

Skull Measurements (mm) of Least Weasels
Dimensions Follow Hall (1951)

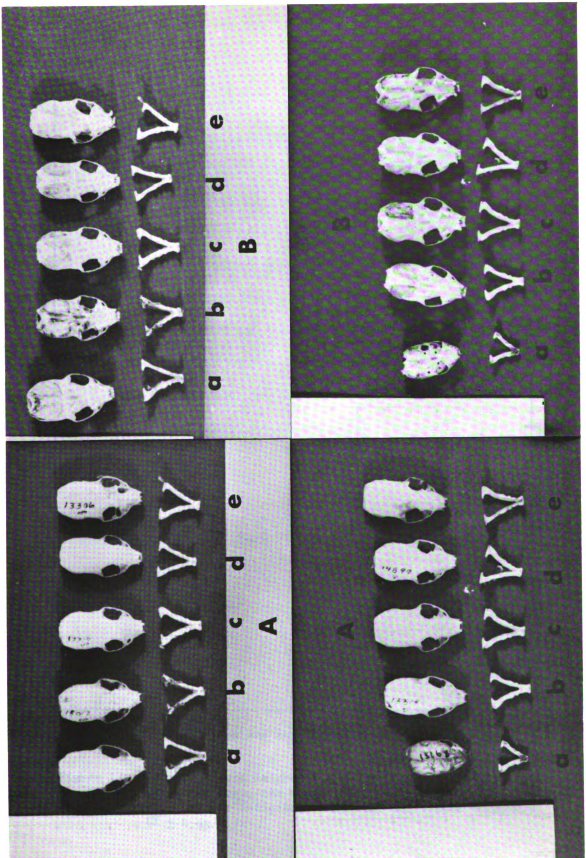
L.W. #	Sex	Age (month)	Basilar Length	Length of Tooth Rows	Breadth of Rostrum	Interorbital Breadth	Orbitonasal Length	Mastoid Breadth	Zygomatic Breadth
14	♀	1	21.0	5.4	5.1	5.1	4.5	10.8	12.6
2	♂	2	30.1	9.7	7.0	10.7	14.8	16.8	10.9
20	♂	3	30.2	9.3	7.4	10.2	14.5	17.6	10.6
21	♂	3	30.7	9.5	6.4	10.2	14.7	17.3	10.5
23	♀	3	29.0	9.4	5.9	6.0	9.6	13.4	15.2
16	♂	5	29.0	9.4	6.5	9.5	14.1	16.8	10.4
17	♂	5	29.4	9.4	6.3	9.8	13.6	16.4	10.0
18	♂	5	29.9	9.4	6.1	9.7	14.2	17.2	10.5
15	♀	5	30.2	9.7	7.5	6.7	10.1	15.2	17.9
9	♂	8	29.8	9.4	7.1	10.1	14.0	16.3	10.8
12	♂	8	30.0	9.4	6.7	10.0	14.2	17.5	10.5
8	♀	8	28.7	9.1	6.8	6.2	9.9	14.0	16.5
10	♀	8	29.3	9.4	7.1	6.3	10.3	14.2	16.7
6	♂	12	28.8	9.4	6.1	9.0	13.7	15.7	10.2
4	♀	12	29.4	9.2	6.6	6.4	9.6	13.4	17.0
2	♂	12+	29.7	10.0	6.6	10.5	15.2	17.9	10.3
3	♀	16	28.4	9.2	6.7	6.5	9.2	12.8	16.2
1	♂	24+	30.3	9.4	6.4	10.3	14.6	16.2	10.8

Table 9. (continued)

Tympanic bulla Length	Breadth	P_4 Lateral	Medial	M. Breadth	Length	Depth of Skull at ant. Basioccipital	Depth at post. Msl	Height of Sag. Crest
7.4	3.9			not	emerged	7.3	5.1	
5.6	3.6	3.8	3.6	1.0	6.7	9.6	7.7	.1
5.7	4.2	4.0	3.7	1.0	7.0	9.8	8.2	.5
5.5	3.6	4.1	3.8	1.1	6.6	9.8	7.5	.6
10.0	5.7	3.3	4.1	1.1	3.2	9.6	7.4	.1
5.7	3.6	3.8	4.1	1.0	6.4	8.0	7.5	.4
5.6	3.6	4.3	3.6	1.0	6.7	9.0	7.3	.7
5.7	3.6	3.8	3.6	1.0	6.6	9.4	7.9	.5
11.0	6.3	3.8	4.4	1.2	3.7	9.6	8.0	.4
6.4	3.5	4.2	3.8	1.0	6.5	8.9	7.7	1.0
5.8	3.5	4.2	3.8	1.0	6.8	8.0	7.9	1.2
10.0	5.6	3.2	3.8	1.1	3.3	9.8	7.3	.2
10.1	5.7	3.5	4.0	1.3	3.3	9.3	8.2	.4
5.5	3.7	4.1	3.5	1.0	6.2	9.3	7.4	.7
10.8	6.2	3.8	4.1	1.1	3.6	9.5	7.7	.2
6.2	3.6	4.7	4.2	1.2	7.1	8.2	8.0	1.5
10.1	6.1	3.3	3.8	1.0	3.9	8.1	7.0	.9
6.1	3.4	4.1	3.7	1.1	6.9	8.1	7.6	1.0

Figure 14. Skulls of female least weasels. (a) One month of age. (b) Three months of age. (c) Five months of age. (d) Eight months of age. (e) Twelve months of age. (A) Dorsal view. (B) Ventral view.

Figure 15. Skulls of male least weasels. (a) Three months of age. (b) Five months of age. (c) Eight months of age. (d) Twelve months of age. (A) Dorsal view. (b) Ventral view.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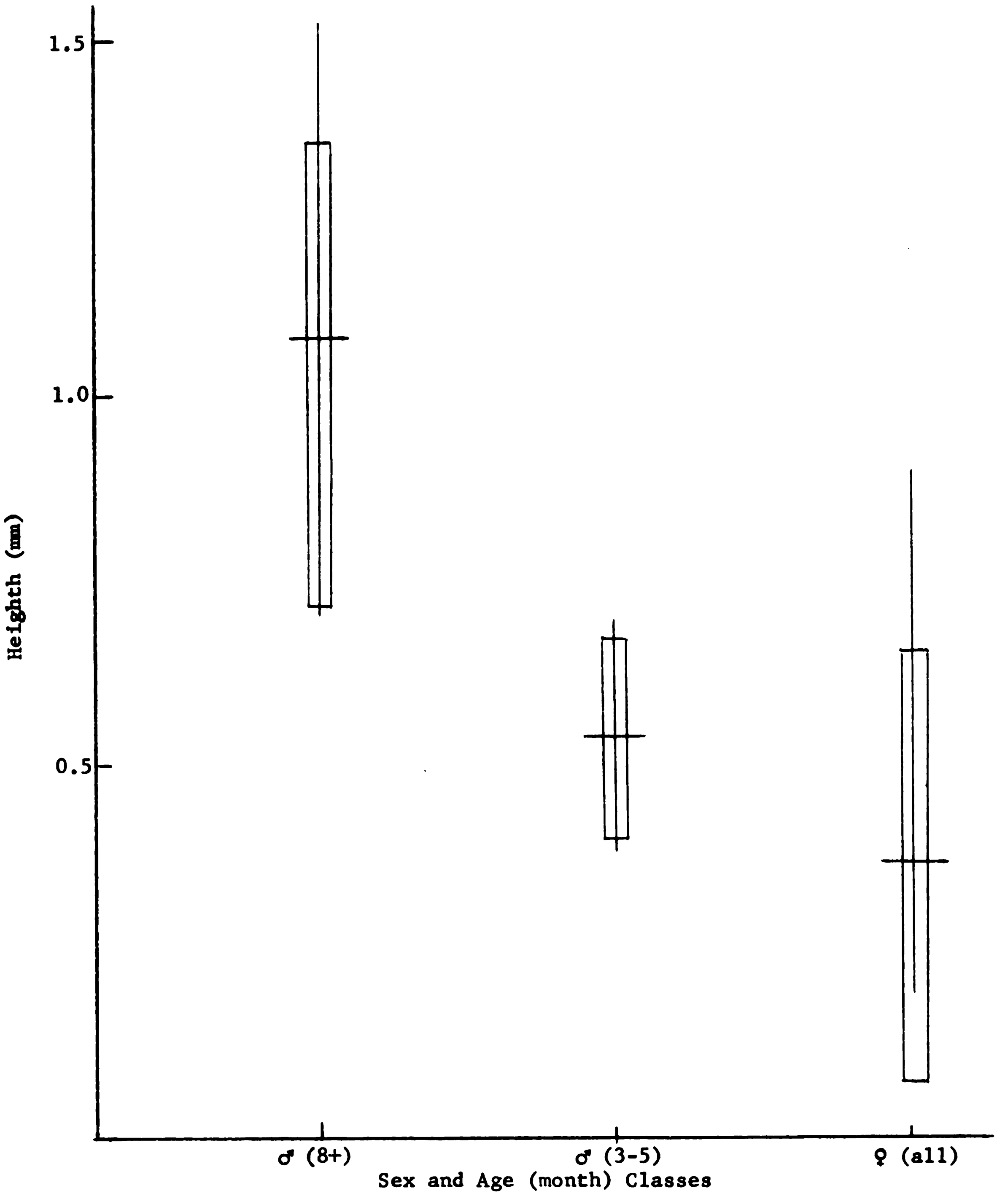


Figure 17. Sagittal crest heighth for *M. nivalis*. The horizontal line indicates mean, the vertical line indicates range, and the vertical bar indicates 95 percent confidence intervals ($\bar{X} \pm t_{.05}\ S_{\bar{x}}$).

Anatomy of the Reproductive Tract

Male

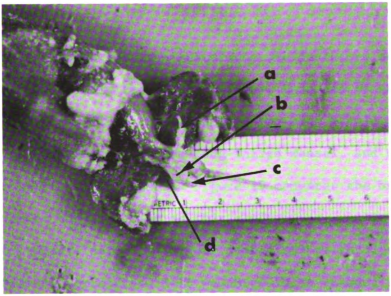
The male reproductive tract (Fig. 17) is comparatively simple, as in the other mustelids and most Carnivora. There are no seminal vesicles and no prostate gland. The testes become scrotal at around 40 days of age and remain in this position throughout the year. Immediately adjacent to the tail of the epididymis the vas deferens is slightly convoluted and reaches its greatest diameter. It continues beyond this point as a thin narrowing tube which crosses over the urethra almost at its junction with the neck of the bladder. There are poorly developed ampulliform swellings formed at the terminal positions of the vasa. Immediately behind the openings of the vasa, the urethra is slightly thickened. A detailed description of the penis (sub-adult) can be found in Long (1969).

Female

The female reproductive tract (Fig. 18) is similar, except in size, to the other mustelids under consideration. The ovaries are flattened and enclosed by a capsule surrounded by the oviduct. The surface of the ovary is smooth except if functional corpora lutea are present, which project conspicuously. The uterus is bicornuate, with the uterine horns beside each other for a short distance and then fusing, forming a single cervical canal. The vagina terminates in a vulval swelling which enlarges during estrus. The mammary glands are abdominal with four pairs of mammae which are inconspicuous in the non-parous animal.

Figure 17. Reproductive tract of male least weasel. (a) Penis, (b) Epididymis, (c) Testes, (d) Vas deferens.

Figure 18. Reproductive tract of female least weasel. (a) Ovary, (b) Oviduct, (c) Uterine canal, (d) Cervical canal.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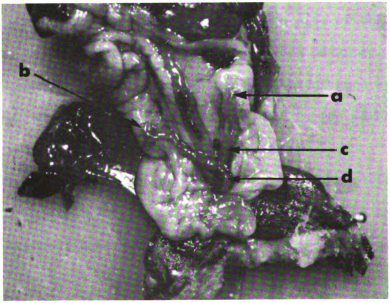
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Ontogeny of Reproduction

Male

Baculum

The bacula of North American Mustelidae are described by Burt (1960). More particularly Lechleitner (1954), Long and Frank (1968), Elder (1951), and Paul (1968) have examined the mink baculum, Wright (1947, 1951) has examined it in the long-tailed weasel, and Deanesly (1935) in the short-tailed weasel. Figure 19 compares the bacula of the five species under consideration in this study.

Table 10 presents data for various dimensions of the least weasel baculum. Pearson's Correlation Test was used in an attempt to correlate the known-age animals with the various measurements. All Figures, except length of the tip, were correlated with age at the .01 level. The breadth at the base showed the highest correlation. As in the other species of Mustela which have been examined, the size of the least weasel baculum is dependent on age and thus sexual maturity. It must be kept in mind, however, that the small sample sizes of each age class in this study may have influenced the results. Due to the method of preparation, weights are not available.

By the age of 3 months the baculum is completely ossified. In the one earlier age class (17 days) examined, the shape of the baculum could be readily discerned; however, ossification had just begun and only various spots along its length had been slightly stained.

Testes

Microscopic examination of the testes from 2 1/2, 13, 20, 32, and 52 week-old individuals was made in an effort to determine the

Figure 19. Comparison of the bacula of North American *Mustela*. (a) *M. vison*, (b) *M. nigripes*, (c) *M. frenata*, (d) *M. erminea*, (e) *M. nivalis*.

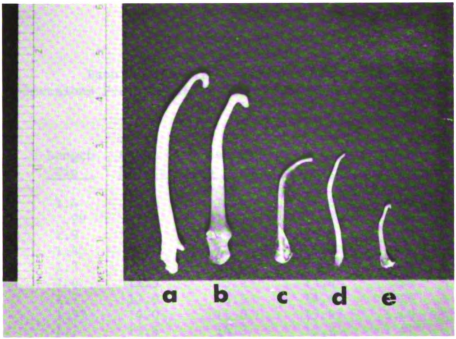
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Table 10

Baculum Dimensions of the Least Weasel
Dimensions From Long & Frank (1968); Measurements in mm.

Age (Months)	Length Tip	Basal Shaft Length	Length Tip to Base	Actual Length	Breadth Base	Breadth Tip
3	1.4	12.2	12.8	13.6	.80	.66
3	.99	12.0	12.9	12.99	.80	.66
5	1.9	12.0	13.0	13.9	.98	.71
5	1.4	12.5	13.0	13.9	.94	.80
5	1.3	11.0	11.9	12.3	.80	.61
8	1.4	12.5	13.2	13.9	.90	.75
8	1.7	12.9	13.5	14.6	.90	.71
12	1.97	14.0	15.0	15.97	1.40	.94
12+	1.7	13.5	14.2	15.2	1.4	.89
24+	1.4	12.5	13.1	13.9	1.1	.75

developmental morphology of the interstitial cells, seminiferous tubules, and spermatogenesis. In many cases the post-mortum freezing of the weasels permitted only gross observations.

In the 2 1/2 week-old young (Fig. 20) the seminiferous tubules were widely separated by intertubular spaces. The interstitial tissue was composed partly of cells with oval nuclei and partly of cells with spindle-shaped nuclei. There were a few locations with small accumulations of larger cells having well-stained nuclei containing one or more nucleoli. These were presumably the cells of Leydig.

The seminiferous tubules, with the exception of one, were small and solid. The one exception was larger than the rest and an apparent lumen could be discerned (Fig. 20). In all tubules one or two layers of cells were found near the basement membrane. These cells had small, round, or oval nuclei and were probably indifferent testicular cells. A few spermatogonia could be observed.

By 12 weeks the histological picture had changed considerably. The seminiferous tubules were prominent and averaged around 180 μ in diameter. All stages of spermatogenesis could be found. However, the number of formed sperms (Fig. 21) was small; some could be seen in the tubules and a few were scattered in the epididymis. Spermatids were common in the tubules. Both primary and secondary spermatocytes could also be discerned. Sertoli cells were numerous and well developed. Hill (1939) found all stages through spermatids in estimated 12 week-old European least weasels, and by the estimated age of 16 weeks some sperm could be seen in both the tubules and epididymis. Hill (op. cit.) also found the seminiferous tubules to average 160-220 μ by the 16th week, which is adult size.

The 20 week-old animals showed a similar pattern to the previous age group, except for the presence of a higher percentage of spermatids and sperm. Details of the tubules were somewhat obscured.

By 32 weeks male least weasels are sexually mature (age at which males first mated). The tubules and epididymis (Fig. 22 and 23 respectively) show the presence of a great many sperm. Much of the remainder of the histology of these tubules resembles that of the three month old group. The male reproductive tracts of the 52 week-old animals appear to be no different from those of the 32 week-old animals.

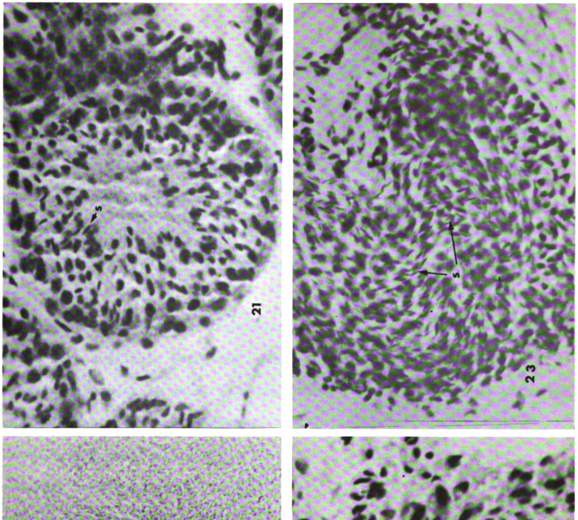
Hill's data (op. cit.) with the estimated ages of European animals appear to be quite similar to the age groups of American animals examined herein. However, Hill was studying the yearly reproductive cycle in addition to the estimated ontogeny, thus his data continue throughout the year rather than comparing different age animals at the same time. Onstad (1967) studying the ontogeny of the mink could not find spermatogonia until 22 weeks of age and spermatocytes through sperm until 28-32 weeks of age. In a later study Bostrom et al. (1968) found similar results with the mink. However, they also found apparent differences in the onset of spermatogenic activity in the different color phases. Spermatogenesis in the short-tailed weasel (Deanesly, 1935) and the long-tailed weasel (Wright, 1947) appear to be similar in that spermatogenic activity does not appear until the spring following birth, which would make the animal 36-40 weeks of age. Wright (op. cit.) correlated this activity with the spring molt in the long-tailed weasel.

Figure 20. Teste of 2 1/2 week old least weasel. Note one large seminiferous tubule on right. (X100).

Figure 21. Seminiferous tubule of 12 week old animal. Note presence of spermatogenesis and sperm (s). (X400).

Figure 22. Seminiferous tubule of 32 week old animal. Note rapid spermatogenesis and large number of sperm (s). Sertoli cells (st) are quite prominent. (X400).

Figure 23. Epididymis from 32 week old animal. Note large number of sperm (s). (X400).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Female

The morphology of the female reproductive organs of the mink has been aptly studied by Hansson (1947), Enders (1952), and Enders and Enders (1963). Deanesly (1935), Watzka (1940), and Lavrov (1944) have done the same with the short-tailed weasel, and Wright (1942a, 1948a) has studied the long-tailed weasel. The most detailed description of the latter two species is that of Shelden (1968). Pohl (1910) and Deanesly (1944) have studied the female reproductive cycle in European least weasels.

Female least weasels comprising 12, 20, 32, 52, and 64 week age-groups were available for study. However, because least weasels are sexually mature at 16 weeks (females have mated at 129 days of age) and the specimens under question were in various reproductive conditions, a chronological study was not feasible. Rather, an ontogenetic study involving anestrus, estrus or near-estrus, pregnant, and lactating individuals was done.

Anestrus

The youngest weasel examined (LW-23) was exactly 12 weeks old at death. At this time the ovary (see Fig. 24) had several follicles in various stages of development but no completely mature graafian follicles. The interstitial cells were numerous and appeared to form tightly packed groups. These cells were generally polyhedral in shape with centrally placed spherical nuclei surrounded by relatively little cytoplasm and resemble those of the other weasels (Shelden, 1968).

The condition of the uterus of this animal (Fig. 25) is similar to that of the anestrus mink (Hansson, 1947), short-tailed weasel (Deanesly, 1935) and domestic ferret (Hammond and Marshall, 1930). Th uterus is small, the mucosa thin and the glands appear compact and relatively undeveloped. The epithelial cells are low and loosely connected.

The histological picture of LW-10, which was 32 weeks of age at death, closely resembled that of the previous animal. This weasel, as LW-23, had never mated. As in LW-23 there were follicles in various stages of development; in one of which the antrum was in the process of forming. There were numerous interstitial cells similar in pattern to the previous weasel.

Estrus or near-estrus

LW-8 was also 32 weeks of age at death; however, she had given birth to one young on 29 April 1968. There was no lactation period since the young had died within 12 hours of birth. The left ovary of this animal (Fig. 26) contained several developing follicles, as well as two large near-mature ones. In addition there was also evidence of follicular atresia in one or two follicles. There appeared to be an extremely degenerated corpora lutea present, perhaps a reminant of the previous pregnancy. The interstitial cells were similar to those described in the previous animals, but were less numerous.

The histology of the oviduct (Fig. 26) and uterus (Fig. 27) were changed considerably from the anestrus state. Both organs were greatly enlarged. The vascularization of the uterus was increased, and dilation of the vessels was apparent. Both the muscularis and mucosa were thickened. Perhaps the greatest change was the enlargement of the gland cells. Their lumina were swollen with large openings, thus noticeably disrupting the continuity of the epithelium.

Pregnancy

Due to damaged preparations no histological study could be undertaken on LW-15, who was 11 days post-coitum at her death. She had, however, mated at 129 days, thus confirming the rapid sexual maturation as proposed by Deanesly (1944).

The other weasel which was pregnant at death was LW-4, who was 28 days post-coitum. This animal was 12 months of age and had bore two previous litters; on 26 November 1967, to five young and 4 March 1968, to five young.

Histologically the left ovary (Fig. 28) contained three large corpora lutea with a mean diameter of 0.70 mm (0.18 mm^3) and the right ovary contained four corpora lutea with a mean diameter of 0.66 mm (0.17 mm^3). In addition several follicles in various stages of development were present. Interstitial cells were still found in groups, however, they were less numerous than in the estrus state.

The oviduct was similar to that of LW-8, in that the lumen, muscularis, and mucosa were enlarged from the anestrus state. There was no histological examination on this, or the subsequent, uteri due to their being used for other purposes.

Lactation

LW-3, who was approximately 72 weeks of age, had given birth to a litter of 6 young, 17 days prior to death. She had previously had four litters (see Table I for details). The histological picture of this animal's ovaries were somewhat obscured by damaged organs. However, it appeared that the corpora lutea, while still active, were rapidly developing into an inactive state. There were a number of follicles present, although most were in the primary stage. One larger follicle appeared to be in a state of atresia. The interstitial cells were more numerous than those found in the pregnant animal.

Figure 24. Ovary of least weasel in anestrus. Note follicular development (f), grouping of interstitial cells (i), and quiescent oviduct (o). (X40).

Figure 25. Uterus of least weasel in anestrus. Note thin mucosa, small lumen, and inconspicuous glans cells. (X100).

Figure 26. Ovary of estrus animal. Note enlarged state of the oviduct (o), the mature follicles (mf), and other follicles (f) in various stages of development. (X40).

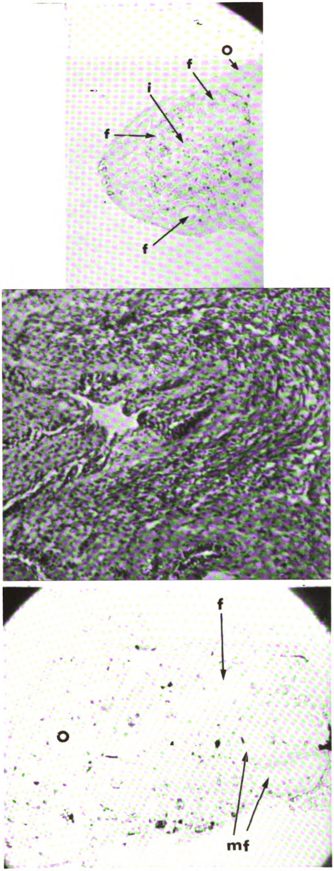
o
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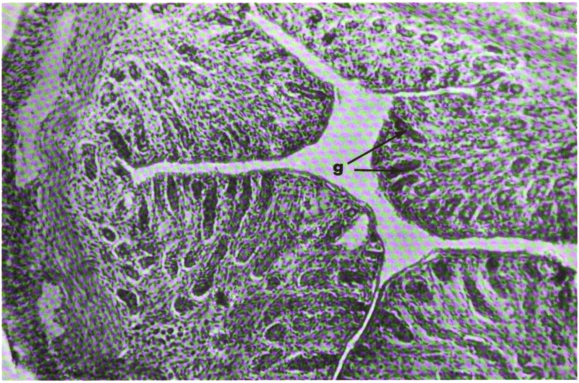
Figure 27. Uterus of least weasel in estrus. Note enlarged muscularis and mucosa, increased vascularization (on left), enlarged lumen, large and conspicuous gland cells (g). (X100).

Figure 28. Ovary of pregnant least weasel. Note enlarged oviduct (o), follicular development (f), and large active corpora lutea (cl). (X40).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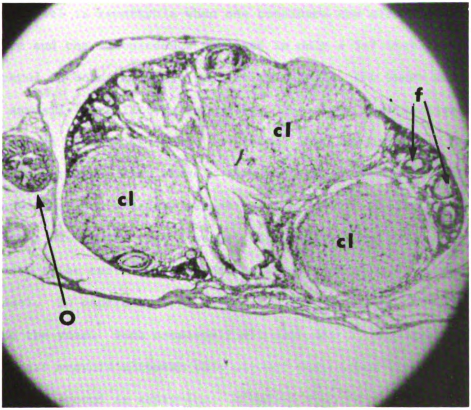
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DISCUSSION

Members of the genus Mustela represent a group of predators which play an important role in the ecosystem. It seems necessary, for this reason, that their biology be fully understood. However, these animals are secretive and wary making them difficult subjects to study in nature. Consequently, it is hopeful that the mass of data presented herein concerning the least weasel's ontogeny and other aspects of its biology, obtained from captive animals, can aid in our understanding of this small carnivore in nature.

From this study it would appear that the least weasel's ontogenetic patterns are similar to those of the other species in the genus considered. The closeness of percentage weight growth between the least weasel and mink is a case in point. For a carnivore, the growth rate of the least weasel is remarkable when one considers the altricial state of the neonate and the independence achieved in only a 5-7 week period.

Compared to other American species of Mustela, the least weasel produces annually more litters and young. In nature reproductive activity may be continuous except in winter, when, according to Hill (1939), male European least weasels show reduced spermatogenic activity. He concluded that the breeding season was thus interrupted during the colder months due to the male's sexual inactivity. Deanesly (1944) found estrus to be curtailed between August and February in the European least weasel. In contrast, Pohl (1910), in Germany, found litters throughout the year. Such complete field data are not now available for Nearctic least weasels although this present work shows that the animals breed the year around in captivity. However, this is not to infer that year-around breeding activity takes place in nature, since it is recognized that reproductive cycles in Carnivora may be modified under influences of captivity (Marshall and Jolly, 1905). A point supporting, but not proving, the idea that continuous breeding may occur in the wild is that a least weasel taken in southern Michigan on 22 January 1969 was judged to be 4-5 weeks of age. This suggested that mating in the field took place in late November. Also Polderboer (1948) found a male least weasel with active testes in late November in Iowa.

As mentioned in the Introduction, delayed implantation has been definitely shown in M. frenata, M. erminea, and M. vison. It is felt that information presented in this study confirms the previous notion that delayed implantation does not normally occur in the closely-related least weasel, M. nivalis. The finding of implanted embryos at 11 days post-coitum, constant gestation periods with actual developmental times similar to those of the other weasels, and the production of two or more litters per year indicate a "standard" mammalian developmental process.

Among placental mammals delayed implantation is an uncommon occurrence. It has so far been found in one or more members of the following eutherian orders: Chiroptera, Edentata, Carnivora, Pinnipedia, and Artiodactyla. However, as a group, species of the family Mustelidae (order Carnivora) exhibit this phenomenon more than any other taxon. Workers through the years have tried to explain the significance of the phenomena and its survival value to the species. From these arguments four basic theories have been proposed.

Fries (1890, 1902) suggested that delayed implantation in the roe deer (Capreolus capreolus) and the European badger (Meles meles) is an adaptation for the benefit of the young. Using only these two species as examples, he argued that the young need to be born as early as possible in spring, so by the next winter they will be sufficiently mature to stand a good chance of surviving. To obtain this time schedule without delayed implantation, mating in these species would have to occur during the winter which is unfavorable to adults. Delayed implantation would thus allow for the times of mating and for birth of young to be at favorable seasons of the year. His theory is designed to fit the patterns in the two species studied but falls short when applied to the condition observed in bears, marten, and the tropical species exhibiting delayed implantation.

Prell (1927, 1930) feels that discontinuous development is characteristic only in 'old' (pre-Pleistocene) genera exposed to the rigors of glaciation. These harsh climatic conditions may have forced a modification in development. Murr (1929, 1931) attacked the ages assigned to some of the genera which Prell termed 'old'. Hamlett (1935) continues by saying that the genera which Prell termed 'new' had ancestors living in the Tertiary just as did his 'old' groups. He further adds, "... it is in the highest degree unlikely that the morphological stability of a genus should be frequently associated with changes in the embryology while genera which have modified their morphology never change the type of development." He then says, "Prell's argument gives me the impression that he has been guilty of Precrustian methods in lopping and stretching facts to fit his hypothesis." Also delayed implantation in tropical species, i.e., armadillo (Dasypus sp.), seems to nullify the argument.

Murr (op. cit.) proposed that delayed implantation arose due to the direct effect of temperature on development. In bears and badgers he thought that it may be the result of the alleged drop of body temperature. In martens and thin-flanked roe deer the organs and glands become chilled. Arguments against this can be seen in the fact that the delay begins in summer and also by the fact that tropical species also exhibit the delay.

In his review of these three theories Hamlett (*op. cit.*) considers the one proposed by Fries to be the only one with merit. He further suggested that delayed implantation is a "useless character" independently developed and without survival value to the species.

Wright (1963) has proposed a fourth theory regarding most northern mustelids. He believes that because the female goes into heat during lactation that a male is attracted to the group in a temporary family relationship at the time the young are being weaned. He points out that the young are weaned at about 5 to 6 weeks of age and reach full growth in three months (see Results section for confirmation) which is a shorter period than many other similar-sized carnivores. Since the young require a large amount of food during this time, it would be a distinct advantage to their survival if the "sex-attracted" male actively helped in providing their food. Seton (1929), Hamilton (1933), and Grigoriev (1938) have reported observations of males of *M. erminea* at the nest and taking food to the young. Wright also points out that females of *M. erminea* have been found pregnant when only two months old; this means that the attending male may breed not only the mother but also her female offspring. In none of these mustelids does the juvenile male reach sexual maturity during the first summer. Wright says "whatever may have been the factors responsible for the evolutionary development of this type of reproductive cycle in northern mustelids, it seems reasonable to consider it an adaptive character having survival value to these species."

When looking over the placental species which exhibit delayed implantation (see Table 11) several important points can be seen. First, most, but not all, are northern mammals. This is a point in favor of Fries hypothesis. Second, most are carnivorous and are high in the ecological food chain; thus they generally do not have a rapid individual turnover and the necessity for more than one litter each year is not great.

I believe that during the early evolution of placental mammals, such modes of development as delayed implantation and delayed fertilization arose independently and in various taxas. It is reasonable to suspect that there would tend to be more numerous examples in groups of closely related genera and/or species (delayed implantation in carnivores and delayed fertilization in bats). If selection pressures, i.e. slow turnover of members or climatic conditions, favored this type of development, then it might become standard in the reproduction of the species. Conversely, if selection pressures, i.e. rapid turnover of members, were totally against such a developmental arrangement then delayed implantation would have been selected against and disappeared.

Mustelids in general are a case in point for the above scheme. Some primitive forms of several closely related groups (i.e., skunks, weasels, badgers, and otters) could have developed delayed implantation in earlier Cenozoic times. Since many mustelids are northern in origin (see Hall, 1951), the climatic conditions along with the "slow" annual turnover of these carnivores might have favored the continuance of this

Table 11

Placental Mammals Which Exhibit Delayed Implantation
(Data from various sources)

	Mammal	Length of Delay and/or Total Gestation Period	
	Order Chiroptera		
	Eidolon helvum - African fruit bat	3 mo.	7 mo.
	Probably other bats		
	Order Edentata		
	Dasypus novemcinctus - nine-banded armadillo	3 1/2-4 mo.	8 mo.
	Dasypus hybridus - mulita armadillo	2 mo. ?	6 mo.
	Order Carnivora		
	Ursus americanus - black bear	5 mo.	9 mo.
	Probably Ursus arctos and Thalarctos maritimus		
Mustelids	Martes americana - Am. marten	224-50 days	359-76 days
Mustelids	Martes martes - beech marten	similar to M. martes	
Mustelids	Martes foina - stone marten	similar to M. martes	
Mustelids	Martes pennanti - fisher	?	327-58 days
Mustelids	Martes zibellina - sable	7-7 1/2 mo.	
Mustelids	Gulo gulo - wolverine	?	215 days ?
Mustelids	Mustela erminea - short-tailed weasel	9-10 mo.	10-11 mo.
Mustelids	Mustela frenata - long-tailed weasel	around 250 days	274-76 days
Mustelids	Mustela vison - mink	varies	40-70 days
Mustelids	Taxidea taxus - Am. badger	6 1/2 mo.	7 1/2-8 mo.
Mustelids	Meles meles - Eu. badger	2 1/2-6 mo.	4-7 1/2 mo.
	Order Pinnepedia		
	General rule except perhaps for Odobenus		
	Example: Phoca vitulina - harbor seal	2-3 mo.	8-10 mo.
	Halichoerus grypus - gray seal	3 mo.	6-7 mo.
	Order Artiodactyla		
	Capreolus capreolus - Eu. roe deer	4 mo.	9 mo.

method of development. These factors acting together might insure the propagation of delayed implantation in those species for which it has enduring survival value. Perhaps those modern groups lacking delayed implantation (i.e., the subgenus Putorius which includes the modern black-footed ferret and European ferret) may never have had this condition or could have lost it, perhaps in the post-Pleistocene period.

This scheme can be used to examine the weasels of the subgenus Mustela in particular. Figure 29 is a diagram illustrating the probable phylogenetic relationships of the American weasels (from Hall, 1951). Delayed implantation might have developed in the primitive stock anywhere from upper Tertiary to mid-Pleistocene. If delayed implantation became a firmly entrenched trait in this primitive stock it might have remained in the more southern long-tailed weasel (M. frenata) when it evolved from the stem stock. This idea might be strengthened if we knew details concerning the reproduction of tropical populations of this species. Of course, the phenomenon has been perpetuated in the short-tailed weasel (M. erminea) which is supposed to represent the stem stock (see Hall, 1951: 61 and Figure 29) and is more northern in distribution.

The distributional pattern of the least weasel would surely be a factor favoring the existence of delayed implantation in this species. However, compared with the larger species the smaller size and lower position of the animal in the ecological food chain probably favored the elimination of delayed implantation (if it were ever present) in its evolutionary development. The least weasel is often sympatric with the other two species of weasels; thus while sharing some of the same enemies it may be preyed upon as well by the other larger weasels (Nelson, 1934; Polderboer et al., 1941). In addition predators not eating the larger weasels (i.e. some birds of prey and snakes) might instead find the least weasel available. These increased mortality factors could cause a more rapid turnover among the population of least weasels, necessitating increased offspring production -- two or more litters per year. This need to have more offspring per year would be a stronger selection pressure against delayed implantation (which would slow down productivity) than the climate would be fore it.

If delayed implantation developed after the least weasel evolved from the primitive stem stock it is reasonable to suppose that this species might never have possessed the attribute, or if it did, the condition very likely was rapidly selected against. If the delay developed in the stem stock before or at the time the least weasel evolved, the separation of the ancestral least weasel from the main stock at that time might be partially explained.

A final point to be emphasized is that in the past all explanations of delayed implantation have been designed to explain the phenomenon as having distinct survival value for propagating the species. It might, however, serve to limit populations of some of the mustelids. Such animals as the long-tailed weasel are among the most efficient hunters and killers in the animal kingdom. The ecosystem might have been easily disrupted and irreparably damaged by an over-abundance of one of these species. Thus, delayed implantation could, in fact, be a factor designed to keep the population levels of these species within ecologically functional limits.

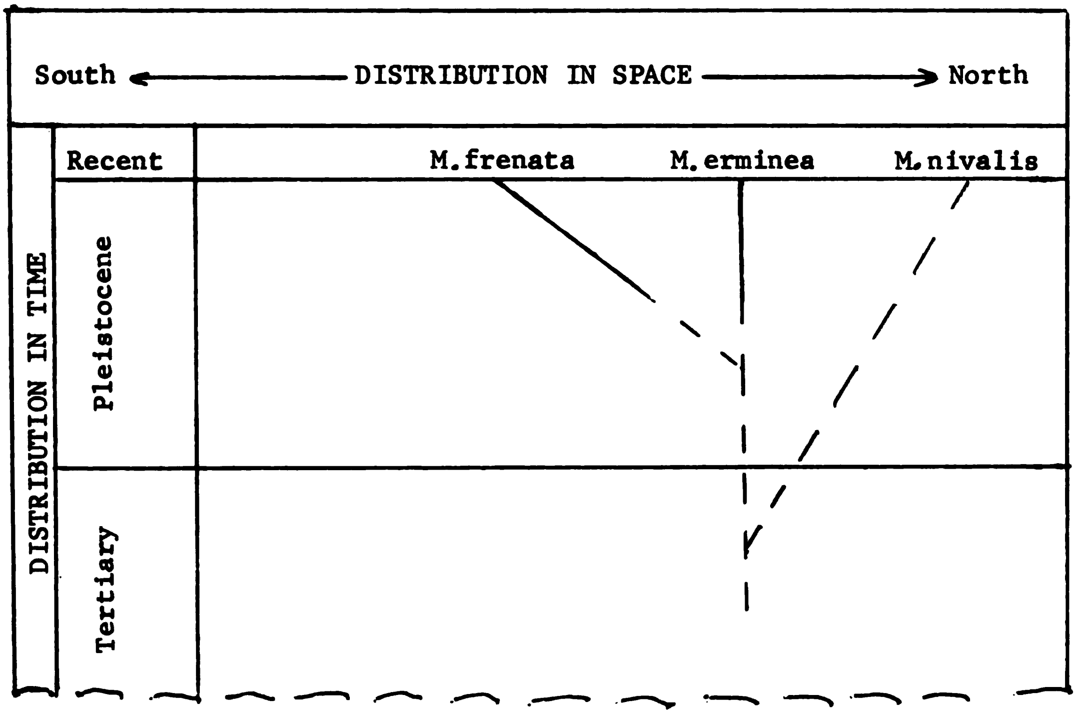

Figure 29. Diagram indicating probable relationships of the species of North American weasels (Modified from Hall, 1951).

SUMMARY

Various aspects concerning the ontogeny of the least weasel (Mustela *nivalis* L.) were examined with laboratory born and raised animals to gain further information about the natural history of this little-known carnivore. These data, included fetal-uterine relationships, litter size, gestation period, neonatal morphology, post-natal morphology, growth, and behavior, and the development of the reproductive organs. The information obtained was then compared to that known (from the literature) about the other four North American species of the genus *Mustela* (*M. frenata* - long-tailed weasel, *M. erminea* - short-tailed weasel, *M. vison* - mink, and *M. nigripes* - black-footed ferret) in an effort to show the relationships between these closely related species, and to attempt to explain the apparent discrepancy concerning the presence of delayed implantation in the long- and short-tailed weasel and mink and its absence in the least weasel.

It was found that in the least weasel two or more litters containing from one to six young are born annually, each after a gestation period of 35 days. The young weigh about 1.42 grams and measure about 48 mm in length at birth. They have an extremely rapid growth, reaching adult length in about 8 weeks and adult weight between 12 and 15 weeks. In size, males of the American subspecies are larger than females but less so than in the Eurasian forms. Least weasels are weaned and can easily kill mice by 6-7 weeks of age. The females reach sexual maturity in about 4 months, while the males first mate at about 8 months.

The litter size of the least weasel does not vary significantly from that of other species of *Mustela*, although the short-tailed weasel

tends to have more young per litter. The actual time of implanted development of the long-, and short-tailed weasel and the mink are similar to that of the least weasel, however, their total gestation periods are considerably longer (mink - 40-70 days, long-tailed weasel - 270 days, short-tailed weasel - 300 days) due to the aforementioned presence of delayed implantation in these species. Percentage growth patterns of the least weasel are similar to those of the mink. Most behavioral patterns examined, in which data are available for all species, (*i.e.* killing techniques) show remarkable similarity between the species.

The four major theories for the development and persistence of delayed implantation are reviewed. It is proposed that while the northern geographical range of the least weasel would favor the presence of delayed implantation as in other *Mustela*, the small size and low position of the animal in the food chain would provide a stronger selection against its presence. It was also suggested that, in general, no theory could be used to explain delayed implantation in all the species which exhibit it. Probably during the evolution of the placental system delayed implantation arose independently (as did delayed fertilization) as a method of development and has persisted only in those forms in which it has definite survival value, or possibly serves as a population-limiting factor.

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APPENDIX A

REPORT OF LABORATORY EXAMINATION

Veterinary Diagnostic Laboratories
Michigan State University
East Lansing, Michigan 48823

Case No. 079263-268

Clinic No.

Received June 4, 1968

Reported June 13, 1968

Veterinarian ______ **Address** ______ **Phone** ______

Owner MSU Museum **Address** ______ **Phone** ______

Specimen 6 dead weasels **Breed** Least **Sex** ___ **Age** adult **Wt.** ______

HISTORY:

These animals were observed all right on the night of 6-3-68 and were last observed between 10 and 11 p.m. At 8 a.m. on 6-4-68 the whole colony was dead. A few of the animals had been vaccinated a few days before for distemper. Animals in an adjacent room were alive and apparently healthy and had been getting the same diet. Other animals in the room were also alive. The room had good ventilation. The diet included laboratory mice and high-protein mink pellets.

GROSS LESIONS:

Four least weasels were posted, and in all of these there were petechial, ecchymotic, and suffusion hemorrhages in the lungs. The kidneys appeared hyperemic. No other gross changes were observed.

LABORATORY FINDINGS:

Microbiologic examination: Stomach contents were taken from 2 least weasels and pooled, and an extract of the stomach contents was not toxic for mice. Stomach contents and intestinal contents had heavy population of hemolytic Clostridium sp. Lungs, liver, and kidney were cultured separately for each of the least weasels, and no growth was reported.

Histopathologic examination: There was extensive congestion of the lungs, liver, and kidneys. There was rather uniform hemorrhage in lung tissue ranging from petechial to suffusion. There was also cortical and medullary hemorrhage in 2 of the 4 animals posted. There was no evidence of inflammation suggestive of an infectious disease. Outside of congestion and hemorrhage, no changes were observed in any organ, including the brain.

Toxicologic examination: Still in progress. Results are not available.

CONCLUSIONS:

Congestion and hemorrhage of the lungs, congestion and hemorrhage of the kidneys, and congestion of the liver.

K. K. Keahey
jf
cc: Mr. Heidt

[signature]
Pathologist

R-414

REPORT OF LABORATORY EXAMINATION

Veterinary Diagnostic Laboratories
Michigan State University
East Lansing, Michigan 48823

Case No. 079263-268

Clinic No.

Received June 4, 1968

Reported July 12, 1968

Veterinarian Address Phone

Owner MSU Museum Address Phone

Specimen 6 dead weasels Breed Least Sex Age adult Wt.

SUPPLEMENTAL REPORT

Toxicologic examination: A report has been received from the Michigan Department of Agriculture, Laboratory Division, Lansing, as follows:

Insecticide residue (housefly bioassay screening) - Insignificant
Pyrethrins - present (less than 2 p.p.m.)

Sample insufficient for further analysis.

COMMENT:

In verbal discussion with the Toxicology Laboratory, the housefly bioassay screening test, there was a die-off of approximately a value 9.4 and, according to their scale, less than 10 is not significant. I think that the presence of pyrethrin in weasel food taken from the cage may be of significance.

K. K.Keahey
jf
cc: Mr. Heidt

Pathologist

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