MUSKRAT PELT PATTERNS AND PRIMENESS

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By

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My thanks also go to all past personnel of the Fur Research Project, especially Robert Dorney, Harold Hettrick, Alan Rusch and Robert Dreymiller, whose efforts, often involving long hours and considerable physical discomfort, resulted in obtaining our large known-age sample of tagged muskrats; to Robert Dobbratz and other members of the Horicon Marsh Wildlife Area staff, both past and present, who checked in the daily catches of muskrats and put in extra effort to locate tagged animls; and to Cyril Kabat, for reviewing the initial outline of the report, and Robert McCabe for reading and commenting on the manuscript.

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ABSTRACT

1. A study of hair growth and pelage changes in muskrats from Horicon Marsh, Wisconsin, has resulted in revision of the traditional concept of the priming process. Pelt collections used in this study included: 868 pelts from immature, known-age muskrats and 85 pelts from known-age adults taken during the regular fall and winter trapping seasons; 143 summer-trapped pelts of unknown-ages; and 33 nestling kits between 1 and 30 days old.

2. The sexing and aging techniques of Shanks (1948) were found applicable to Horicon muskrats with an error of less than 2 per cent. The degree of pigmentation in adult pelts could not be used to determine precise age.

3. Four easily recognizable patterns seemed to recur constantly throughout all immature age groups, and were designated by the Roman numerals I, II, III, and IV. All other patterns could be considered as variations of one of these four. Completely dark pelts were designated as "O" and completely white pelts as "V".

4. Because of the repetition of patterns in immature animals, and the individual variations in patterns and time of occurrence, a practical aging technique based on immature pelt patterns could not be devised. Likewise, pelts could not be dated according to the time of the year they were taken by basing the technique only on flesh patterns.

5. The primeness process is *not* a simple matter of new hair growth occurring in the fall and progressing toward eventual prime in the spring, as formerly believed. Rather, hair growth occurs in a succession of wave-like growths, each one complementing the previous one until the prime condition is reached.

6. This conclusion was first substantiated through gross examination of immature muskrat pelts. The frequency of occurrence of the four basic patterns showed a fluctuation from dark patterns to light patterns and back again. While all four patterns could be found for any particular age group, one pattern was always dominant for that age group.

7. Further substantiation of the growth wave concept was furnished by studies of pelage changes in captive muskrats following shearing. Up to seven separate hair growths were found in these animals before they were one year old. Most of the animals began and completed growths at approximately the same ages, even though they were not all litter mates. The rapidly forming symmetrical hair growths of young muskrats gradually slowed and became increasingly irregular as the animal grew older.

8. Certain forms of physical stress such as insufficient diet, sickness, pregnancy, and parturition had a suppressing effect on hair growth. Pattern irregularities many times are associated with scars due to old wounds to the skin, indicating that injuries can modify the manner of hair replacement. Under normal circumstances the effects of weather on hair growth are of minor importance.

9. Hair growth was divided into developmental and seasonal types. Developmental hair growth occurs only in immature animals. It is dependent on the age and physical condition of

the animal but not on the time of year or the weather. Nestling, juvenile, post-juvenile, and subadult pelages are all developmental hair growth.

Seasonal pelage changes are restricted to adult muskrats and the late transition period between adult and immature growth phases in the spring. The flesh surfaces of pelts are covered by an irregular blotchy growth pattern in contrast to the symmetrical patterns of the developmental pelages. Seasonal growths can be divided into spring, summer and winter pelages in the adult muskrat.

10. As a result of this study, primeness has been re-defined as *that condition of the pelt existing when the pelt is at its highest quality and the fur has reached its maximum length, density, and finest texture; when the hairs have matured with seemingly no further pigment being produced, and as a consequence, the flesh surface of the pelt appears devoid of hair root pigmentation.* A pelt is prime only when a combination of all these factors is present, and a pure white pelt is not in itself sufficient evidence of primeness.

CONTENTS

INTRODUCTION

The ultimate objectives of muskrat (*Ondatra zibethicus*) management are to produce the maximum number of muskrats consistent with the capacity of the habitat, to efficiently harvest the surplus and to obtain the maximum monetary returns for this harvest. Planning a harvest is most efficiently accomplished when the factors affecting maximum pelt values are properly considered and are well understood. Value of the harvest is controlled by supply and demand in the fur market and by the quality of the pelts which make up the harvest.

Pelt quality is dependent on the preparation and care of the pelt and on the degree of primeness of the pelt. Since primeness is considered by trappers, fur buyers and game managers to be of major importance in determining quality and price, it is necessary to know what constitutes a prime pelt, what factors affect primeness, and how primeness takes place. The process of molt and hair growth, primeness, and the pigmentation of the skin and pelage are all interrelated, and an understanding of any one is helpful in understanding the others.

Hair growth and pelage changes have been a controversial subject for a great many years. Sir Thomas Pennant (1784) studied the seasonal color changes in the pelage of the snowshoe hare *(Lepus americanus)* and stated that changes come about by the production of a new growth of hair. Pennant's views were supported by Allen (1894) and Grange (1932). Welch (1869) and Hadwen (1929) took issue with these views, believing that the change was occurring in existing hairs.

Hollister (1911) observed that coastal muskrats have two molts while all other muskrats have only a single molt. However, he offered no detailed description of the progression of changes occurring.

Gunn (1932, 1933) worked out a theory concerning primeness in muskrats and other animals on the premise that mature or prime hairs blanch at their bases in all animals except albinos. The distance that these hairs blanch varies from species to species with the extreme condition being found in those animals showing seasonal color variations. In these cases he suggested that, "... autumnal color change is due to blanching of the summer coat or is merely an exaggeration of the same condition" (p. 558).

Gunn's (1932) histological study of muskrat pelts is one of the most comprehensive yet undertaken on the subject. He attempted to correlate seasonal changes in the appearance of the flesh surfaces and pelage of pelts with his own detailed histological observations. Prior to this time, studies on hair growth in muskrats were noticeably lacking.

Lavrov (1944) was the first to mention the difference between adult and immature flesh-side pigmentation patterns. He noted that adult pelts showed a blotchy mosaic pattern and immature pelts were linear or striped in pattern. Kellogg (1946), apparently unaware of Lavrov's findings, stated that he suspected a difference between adult and immature patterns, but had insufficient material to prove it. Applegate and Predmore (1947) confirmed Kellogg's ideas.

Shanks (1948) showed the reliability of using pelt patterns for aging muskrats through use of known-age pelts. He credits Buss (1941) with discovering that only pelts from female muskrats showed teat marks on the flesh surface, thus making it a relatively simple matter to sex the pelt.

Beer (1949) also advocated the pelt-pattern method of aging animals. Based on a sample of 21 known-age muskrats and a large number aged on the basis of reproductive tracts, he attempted without success to work out a sequence of prime. In some of these and other studies, attempts were made to follow the direction and manner of prime and to determine the effect of the seasons. A lack of sufficient known-age material in all cases gave questionable results.

Ever since Gunn (1932) wrote his *Phenomena of Primeness*, the degree of pigmentation on the flesh side of a pelt has been considered directly indicative of the degree of primeness of the pelt. Accordingly, a late summer pelt should be completely dark (Gunn, 1933) on its fleshy surfaces, but should grow progressively lighter from ventral regions to dorsal with the approach of fall and winter, until finally in March it should become completely white when the pelt is fully prime. Gunn (1932) stated that dark coloration of the flesh side is caused by the massed effect of growing hairs which contain pigment in their roots, and is not due to any pigmentation of the dermis itself. Primeness, which is associated with the white condition of the flesh side, is due to blanching of the hair roots.

Applegate and Predmore (1947: 325) wrote, "The conventional method of determining the prime and unprime areas on the flesh side of a muskrat pelt is a visual one. The blue-black or black pigmented areas are unprime and the creamy white unpigmented areas are prime. . ."

OBJECTIVES

Because the existing literature has inconsistencies regarding the nature of hair growth and primeness, we undertook a study to clear up these discrepancies. Our muskrat litter-tagging for population studies of Wisconsin muskrats made a large number of known-age pelts available during fall and winter trapping seasons. Our major objective was to obtain a better understanding of the primeness processes so that trappers, fur buyers, game managers and law enforcement officers would have a common ground on which to judge the quality of pelts.

Other objectives were as follows:

1. Determine the factors affecting the formation of pigment patterns on the flesh side of pelts, and determine their relation to primeness.
2. Determine the accuracy of aging muskrats by pelt patterns and of sexing by teat marks.
3. Develop an aging technique for immature muskrats based on pelt pigment patterns.
4. If accurate aging is not possible by pelt patterns, determine if patterns can be used for classifying litter production on a monthly basis.
5. Determine if pelt patterns have value in law enforcement cases where the time of year a pelt was taken must be established.

METHODS

Study Area

All muskrats used in this study were taken on the 10,000-acre state-controlled portion of Horicon Marsh in Dodge County, Wisconsin. Water levels on the marsh are controlled by a dam across the Rock River in the city of Horicon, and maintained to produce optimum habitat for waterfowl, furbearers and other aquatic wildlife. Principal vegetation consists of cattail, burreed, river bulrush, and hardstem bulrush in the deeper portions, with sedge and grass associations in the shallower peripheral areas.

Fur trapping on this area is on a strictly controlled share-trapping basis, with two-thirds of the catch for the trapper and one-third going to the State. The trapping season starts in late October or early November and continues until either an adequate harvest is taken or until weather conditions make further trapping impracticable.

Pelt Collections

A major portion of our data is based on pelts from known-age muskrats ear-tagged as nestling kits. Tail lengths and sex were recorded at the time of tagging. Kit ages were determined from tail lengths using the methods of Dorney and Rusch (1953). A total of 953 known-age pelts was collected during the years 1950, 1951, 1953, 1954 and 1955. Additional tagged pelts obtained in succeeding years were used as a cross check. All known-age pelts used in this study were originally tagged at ages from 12 to 30 days, so that any error in aging is relatively small. Tag returns were obtained when share-trappers checked in their daily catch at the Horicon Marsh headquarters. Pelt file cards were made up containing information on tagging date, birth date, return date, age at return, sex and tag number. Each pelt was photographed from both dorsal and ventral sides and the enlarged prints pasted to the file card.

Summer trapping by the author supplied 77 pelts in 1954 and another 66 in the summer of 1955. This collection contained both adult and immature pelts. It provided a series of adult pelts with which to trace summer adult patterns. Relatively few of the immature summer pelts were of known-age, so their use was restricted to making comparisons by size and date of capture. While such comparisons do not have accuracy, they do give an indication of what may be happening in the age groups below 100 days of age where the main known-age collection is weak or lacking.

In 1955, nine litters containing four or more kits each were litter tagged and their houses marked to facilitate making recaptures. One kit was collected from each of these litters at the time of tagging, and it was hoped to make recaptures at weekly intervals, thereafter. However, low water levels made conditions unfavorable and only four recaptures were made from four different litters. All further returns were obtained during the regular trapping season after the kits had become large immatures. This, of course, did not yield the desired sample in the younger age groups.

Twenty-two nestling kits were collected during litter-tagging operations in 1954, and another 11 were taken in 1955 to provide information for the period from 3 to 30 days of age. The kits were skinned in such a way that they could be later made into skin mounts. The pelt after removal was turned flesh side out and the pigment pattern was diagrammed. After a thorough study of the flesh side, skin mounts were made so that a permanent record of the pelage was obtained. Using these skins, the progression of kit hair growth was studied in some detail with the aid of a dissecting microscope.

Sex and Age Studies

Applegate and Predmore (1947), Shanks (1948), and Beer (1949) have reported on the practicability of using pelt patterns as a means of aging muskrats. Because of the differences in locale and the fact that these investigators had used, at the most, a very small sample of known-age pelts, we checked the technique using known-age Horicon pelts.

All pelts obtained from trappers were assigned a number and all other marks identifying the pelt were removed. For ease in record keeping, a pelt identification key was compiled listing the original ear tag number and the new pelt number. This identification system allowed appraisal of the pelts without bias.

Hair Growth and Follicle Studies

In attempting to trace changes in pigment patterns on the flesh side of pelts, it became obvious that these patterns were a direct reflection of hair growth taking place on the hair side, as Gunn (1932) contended. To illustrate these changes more clearly, one-eighth-inch strips were cut through the skin around the girth of the pelt approximately one-half inch anterior to the tail. The resulting circular strip was then cut open and placed between two pieces of glass to hold the hair flat and make observations easier. On unusually heavy pelts, differences in hair density could be more easily seen if the strip was sectioned narrower than one-eighth-inch.

Limited checks were made on hair follicles from the dorsal areas of selected pelts to determine changes in hair density and hair production with age, and the effects of seasons. This was accomplished by dissecting out compound follicles under a binocular dissecting microscope with a piece of sharply pointed safety - razor blade. The dissected follicle complete with hair was then transferred to a slide and examined under a conventional microscope. Twelve known-age muskrat pelts of varying ages were selected for this study.

Experiments With Live Muskrats

To provide further cross checks on the development of pelt patterns, experiments were carried on with live animals using hair bleach, hair dye, and shearing to delineate new pelage growths.

All animals were periodically examined and photographed in color to provide a permanent record of the changes occurring. Black and white photographs were not satisfactory. Cumulative notes were kept on each pen-raised muskrat. These included weight, tail length, written description of the animal's appearance, and a sketch or diagram of the growth pattern, plus brief notes on occasional histological samples of the hair, and other pertinent information.

At the conclusion of the study, all color slides were assembled and labeled for each kit. Then they were projected on 8½-by-11-inch paper and the outlines traced. Semi-diagrammatic sketching of the pattern growths produced a useful means of portraying the changes taking place and offered a more versatile means of studying them. When the entire sequence of drawings for a particular kit was assembled, it was possible to study in detail the growth that had occurred from 30 days of age until death of the animal the following spring.

In the fall of 1956, one adult and five immature live-trapped muskrats were used in hair bleaching and dyeing experiments to see if artificially colored fur would produce a contrast with any new hair growth so that hair replacement patterns could be followed. Bleaching and dyeing, as techniques for following molt patterns, have been used successfully on pocket gophers by Morejohn and Howard (1956), and on domestic rabbits by Whiteley and Ghadially (1954). A preparation commonly used by beauticians on human hair called Roux Quick Bleach Powder dissolved in 20 per cent Roux Bleaching Peroxide was used to bleach three immature muskrats. The remaining three animals were dyed black using another Roux product prepared for human hair.

Although pelage of penned muskrats could be bleached or dyed successfully, pelage changes were difficult to follow because of the gradual and diffuse manner in which changes occurred. The trouble encountered in interpreting changes seemed due to the fact that growths of new hair accounted for only part of the hairs in each follicle, while the remainder were bleached or dyed old hairs that were retained and tended to mask new growth. Bleaching and dyeing were judged unsatisfactory techniques for following hair growth patterns.

Shearing experiments were carried on with three pen-raised litters whose litter sizes were one, two, and six kits. These were supplemented with a wild litter of three kits captured at 21 days of age. The two smaller pen-raised litters were first discovered in the nest at estimated ages of two and five days. The litter of six was found within a day after it was born. Just after the first nestling coat was completed, pen-raised kits were completely sheared except for the head. All succeeding growths were carefully recorded. Each time a growth was completed the animal was again sheared. Small sections of new growth areas sometimes showed delays in the occurrence of new growth of hair. In such cases the surrounding areas that had produced hair were sheared and a narrow edge of long hair was left to delineate the delayed areas. These incomplete sections were then left until a new growth covered them. If the entire growth area completed its coverage slowly, a narrow strip was sometimes sheared around the girth of the animal in the region where new growths were known to begin. This made it possible to observe when new hair growths occurred before the preceding one was completed. The animal was later sheared throughout the growth area.

An attempt was made to determine what effect plucking hair would have on subsequent hair growths. Dawson (1930), Butcher (1951) and other workers stated that plucking stimulated hair growth and caused an early growth of new hair. We made a superficial check to see if forced hair growths could be obtained in muskrats. Four penned muskrats were plucked bare on the rump region. Pluckings covered areas about the size of a nickel. They were plucked immediately after the mid-dorsal region had been sheared so that any advanced new growth would be clearly delineated against the surrounding sheared pelage.

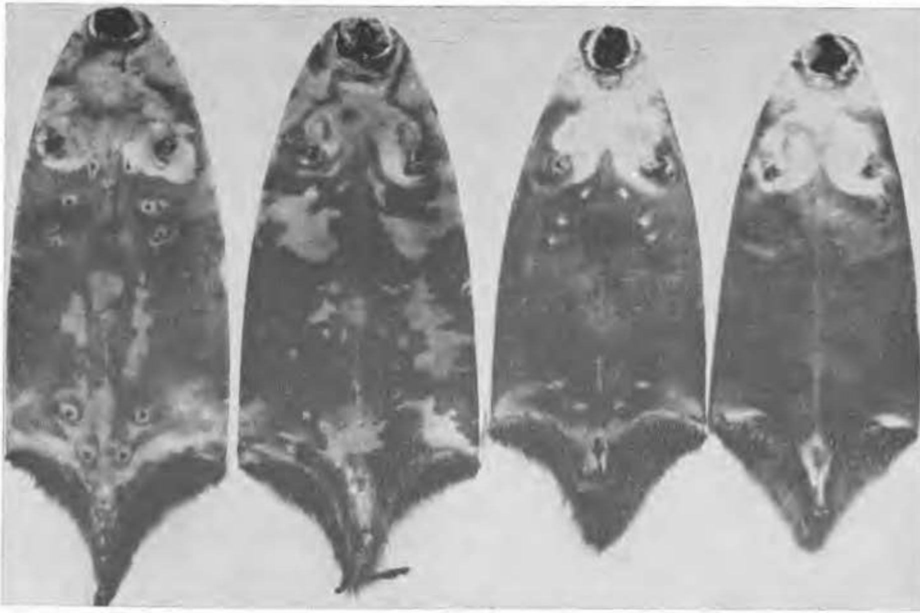
PELT PATTERNS IN RELATION TO AGE AND HAIR GROWTH

Sexing and Aging by Pelt

The method for determining sex and age by pelt patterns (Buss, 1941, Applegate and Predmore, 1947, Shanks, 1948) is shown in Figure 1. Shanks stated, "The majority of primeness patterns are definitely one of two types: first, the symmetrical pattern of the sub-adult; second, the mottled pattern of the adult" (p. 182). The adult pelts in Figure 1 have an irregular, blotchy, mosaic type of pattern. By contrast, immature pelts have large areas with solid blocks of color and the dorsal pattern is symmetrical and linear.

Sex is determined by the presence or absence of teat marks. In Figure 1 the adult and immature female pelts exhibit 10 well-defined teat marks; 6 pectoral and 4 inguinal. Neither of the male pelts show any visible mammary markings.

Shanks (1948) reported that 10 per cent of his Missouri pelts had an intermediate pattern and were hard to classify for age. Preliminary examination of our collection failed to show similar findings. In 1952, Shanks and Mathiak each separately sexed and aged our entire known-age sample of 634 pelts collected during the 1950 and 1951 trapping seasons at Horicon. This collection consisted of pelts from 549 immatures and 85 adults. Their combined check included 19 mis-identifications, or slightly more than 3 per cent of the total collection. This amounted to 9.5 errors per man for both sexing and aging, a relatively small error for this type of technique. In actual practice, the effect of these errors would be somewhat less because they are compensating. This applies both to sexing and aging.



ADULT FEMALE　ADULT MALE　IMMATURE FEMALE　IMMATURE MALE

Figure 1. Sex and age ean be determined from the stretched raw pelt. Blotchy patterns are typical of adults. Immatures show blocks of color ventrally. Teat marks are clearly visible in both the adult and immature females while the two males show no teat marks.

Causes for the few errors which were made were: (1) pelts taken late in the year having little or no pigmentation, and pelts having very dark indistinct patterns; (2) mechanical errors; and (3) pelts difficult to sex. The first type of error accounted for only 3 pelts being aged wrong. When February and March pelts were eliminated from the sample this error was less than 1 per cent. Pelts taken after January include so many white and nearly white pelts due to the beginning of the spring prime period that aging by pattern is impractical.

Mechanical errors are caused by (1) haste in examination, (2) distracting influences, (3) poor pelt preparation and (4) recording mistakes. Shanks and Mathiak made a total of 9 errors of this type, which were slightly more than 1 per cent of the total.

Errors were made in sexing 7 pelts (about 1 per cent) which exhibited indistinct teat marks. Six of these were pelts from immature females, 1 of which actually bore no teat marks at all. The seventh pelt was from an immature male. In some cases only 2 or 3 teat marks out of the normal complement of 10 can be seen in female pelts. It has been observed that a small proportion of the males may also bear one or more teat marks, but these are vague and almost indistinguishable. In most instances they will not be confused with female pelts because the marks are usually so extremely faint.

Our check indicated that from the beginning of the trapping season in October or November into January, muskrat pelts at Horicon can be sexed and aged by the pelt-pattern method with less than 2 per cent error. This method, therefore, offers a rapid yet accurate technique for determining the composition of muskrat populations for population studies and management checks.

An objective of our study was to develop an aging technique for immature muskrats based on pigmentation patterns. Applegate and Predmore (1947: 325) believed that they could subdivide immature muskrats "... into groups partly on the basis of size but primarily on certain characteristics of patterns of prime and unprime pelt". However, their conclusions were based on 64 muskrats of unknown ages which they recognized as an unreliable sample.

After we had learned more about the changes occurring in patterns from our large known-age sample we found we could expect certain general patterns to occur more often in certain age spans than in others and repeat themselves at intervals. This seemed like a possible basis for working out an aging technique. Ecke and Kinney (1956), working with *Peromyscus californicus*, found that using size and pelt pattern together gave a usable aging technique. They stated, "Although there is considerable size variation among individuals the total length of an animal will usually key it to one of the molt phases... Then by noting whether the molt phase is in the early or advanced stage it is possible to age the animal within 4 days of the absolute age" (p. 253).

In muskrats, individual variations make the time of pattern appearance very unreliable and pattern overlap quite large. At the same time, relatively large age spans (up to 27 days) are sometimes represented by a particular pattern, thus making the time of pattern development rather general. To be of practical value, a technique should accomplish aging at least by monthly periods between the ages of 100 to 200 days, which is the period when most muskrats are harvested at Horicon. During this period, patterns are repeating themselves at intervals as will be subsequently shown. When I tried to delineate age groups by associating patterns with pelt sizes and weights to establish age, I found that both pelt size and weight were variables in themselves and only served to introduce further errors. I concluded, therefore, that aging immature muskrats by pelt pattern was impractical.

Pattern Characteristics

Adults

A preliminary examination of 85 known-age adult pelts taken in fall and winter indicated that adult ages could not be correlated with particular pigment patterns. Seasonal influences appeared to have a more pronounced effect than age, although even these changes were gradual and somewhat indefinite. When adult pelts were spread out in order of their dates of capture, no orderly changes could be seen in the pigment patterns from one pelt to the next. However, the collection as a whole indicated an extremely slow and irregular, almost imperceptible lightening of the pelts from the early pelts of late October through the late pelts of March and early April. Although there was a marked difference between the two extremes, it was not possible to arrange the collection

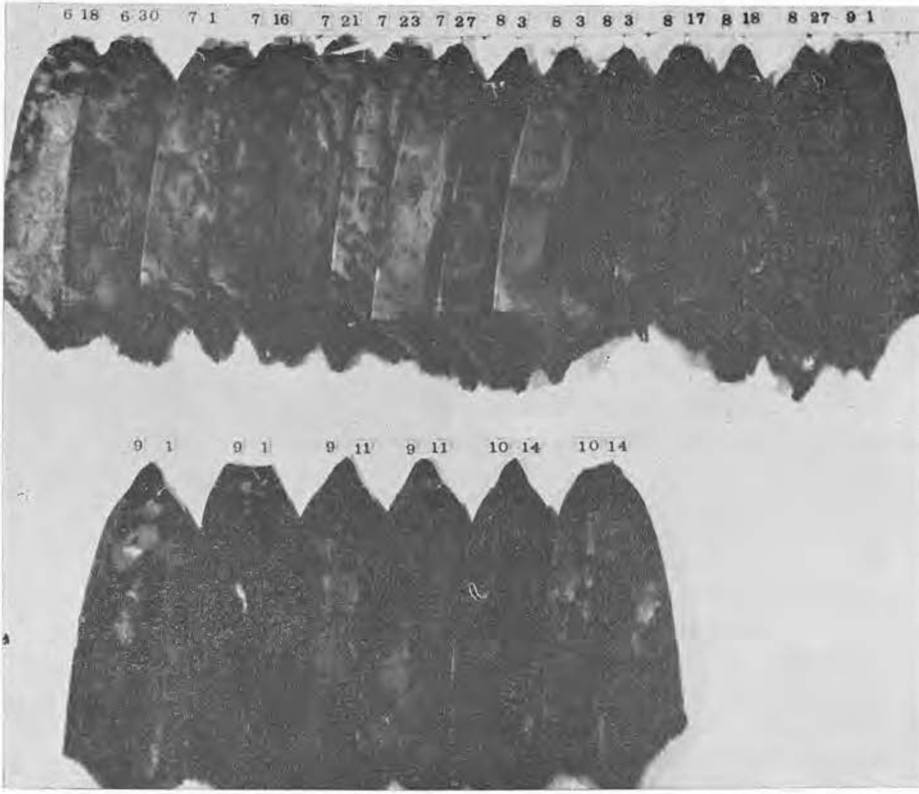
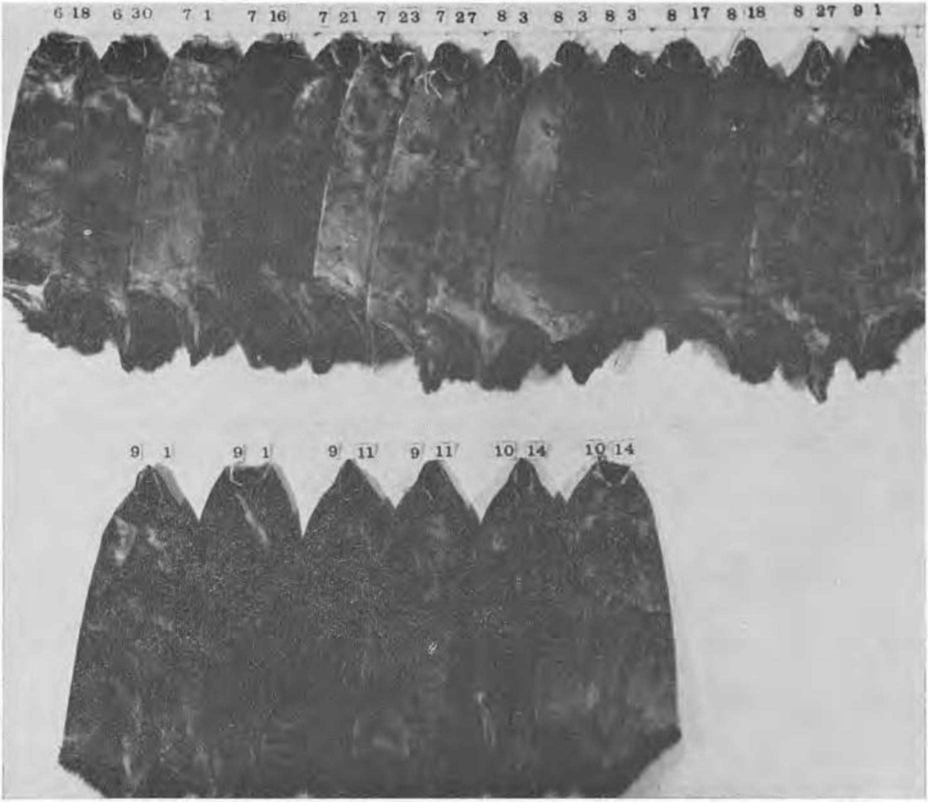


Figure 2. The summer adult series from 1954 in chronological order of capture dates (dorsal view

chronologically on the basis of the amount of pigmentation of the flesh side because individual variations masked gradual changes. Generally skins are the lightest in late February, March and early April, during which time they attain complete whiteness. They begin to show dark spots toward the middle of April when shedding and new hair growth begins once more.

Forty adult pelts taken in the summers of 1954 and 1955 were added to the collection to trace flesh pigmentation during the summer months. When these pelts were put in chronological order of their capture dates, they indicated that pigmented areas appearing in mid- and late April increased somewhat in intensity, but never seemed to reach maximum pigmentation because in late July the pelt began to lighten again until by the middle of August it was once again pure white on the flesh side (Fig. 2). Pelts were found in August with pure white flesh surfaces during both years. Following the white phase, darkening of the skins commenced once more, until by the middle of September the flesh sides of the pelts were at their darkest point for any particular time of the year.

Nearly all the very light summer adult pelts were from females, as were also the very dark pelts. Adult male pelts arranged in chronological order of their collection dates darkened only moderately in June over those taken during the spring period (Fig. 3).



at left; ventral at right). Numbers above each pelt indicate the month and day they were taken.

Through the summer and until September only a relatively small increase in the intensity of pigmentation occurred. From September on, a very gradual lightening of the pelt began.

Adult female pelts placed in chronological order of their collection dates showed a slight amount of pigmentation after the spring prime period, but this was followed in August by a pure white pelt (Fig. 4). Skin coloration increased after this white phase until in September the pelts were very dark. After this dark phase the pigmentation once again began to fade.

Although pigmentation in general was more intense in 1954, collections for 1954 and 1955 were very similar in rate of change.

Immatures

Pattern Irregularities. Photographs of known-age pelts show that irregularities in pelt pattern symmetry begin as early as 164 days of age. At this age it seems to be confined mostly to a streak along the center of the belly. In the 170- and 180-day age groups, irregular blotches make their appearance again, mostly on the belly. The dorsal surface still maintains a linear appearance, although irregularities may show up within the linear pattern. Irregularities continue to increase in the older age groups, until by 216 days of age even the dorsal pattern may become distorted in an irregular fashion. Increasing age and advancing season eventually slow hair growth and dis-

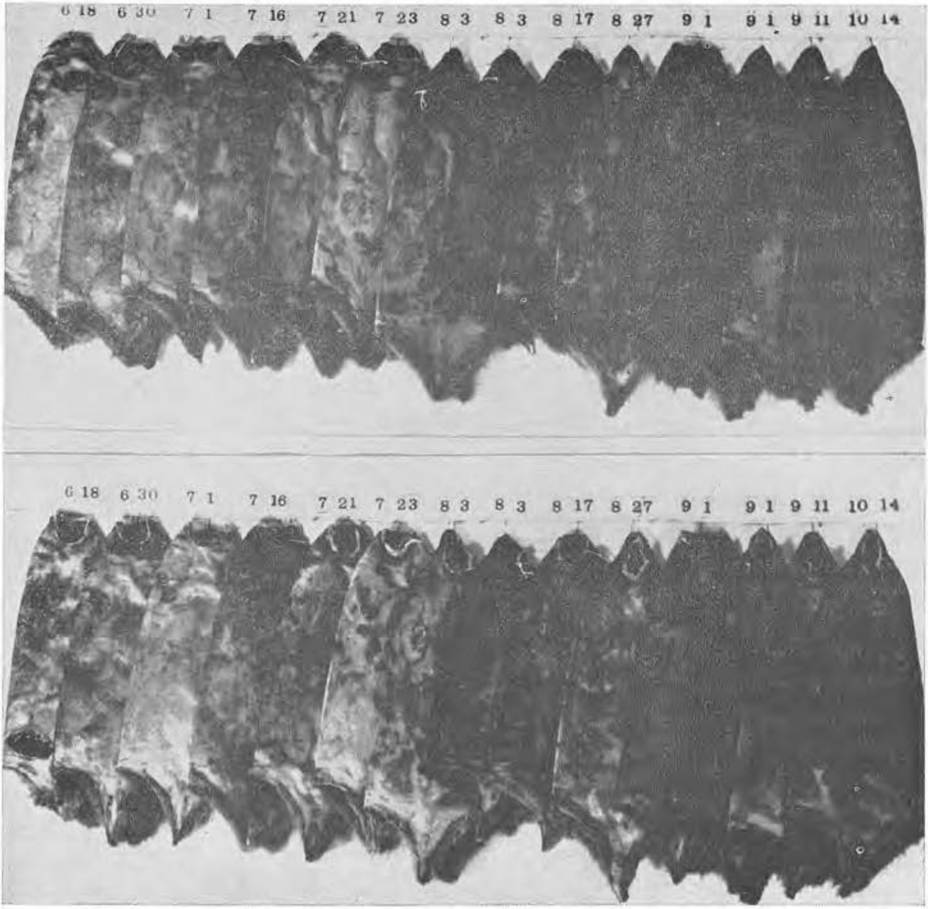


Figure 3. Dorsal (top photo) and ventral (bottom photo) views of summer adult male pelts taken in 1954.

tort patterns so that it is difficult to distinguish between immatures and adults. The amount of distortion and irregularity is to a large extent dependent upon individual variations, even though the trend is as described above.

Exactly what percentage of immature animals attains a typical adult-pattern after December is hard to say. Our tagged animals were returned in very small numbers after the latter part of December. Most of these were taken in March and April and had pelts with completely white flesh surfaces. However, information from our pen-raised kits, which will be presented later, indicates that toward spring adult patterns may be quite common in animals born during the preceding summer.

We have some inconclusive information from yearly sex and age ratios based on pelt patterns which indicates the possible presence of adult-like immature patterns in late pelts. During the years 1948, 1951 and 1954, sex and age ratios were obtained from late pelts taken in December and January.

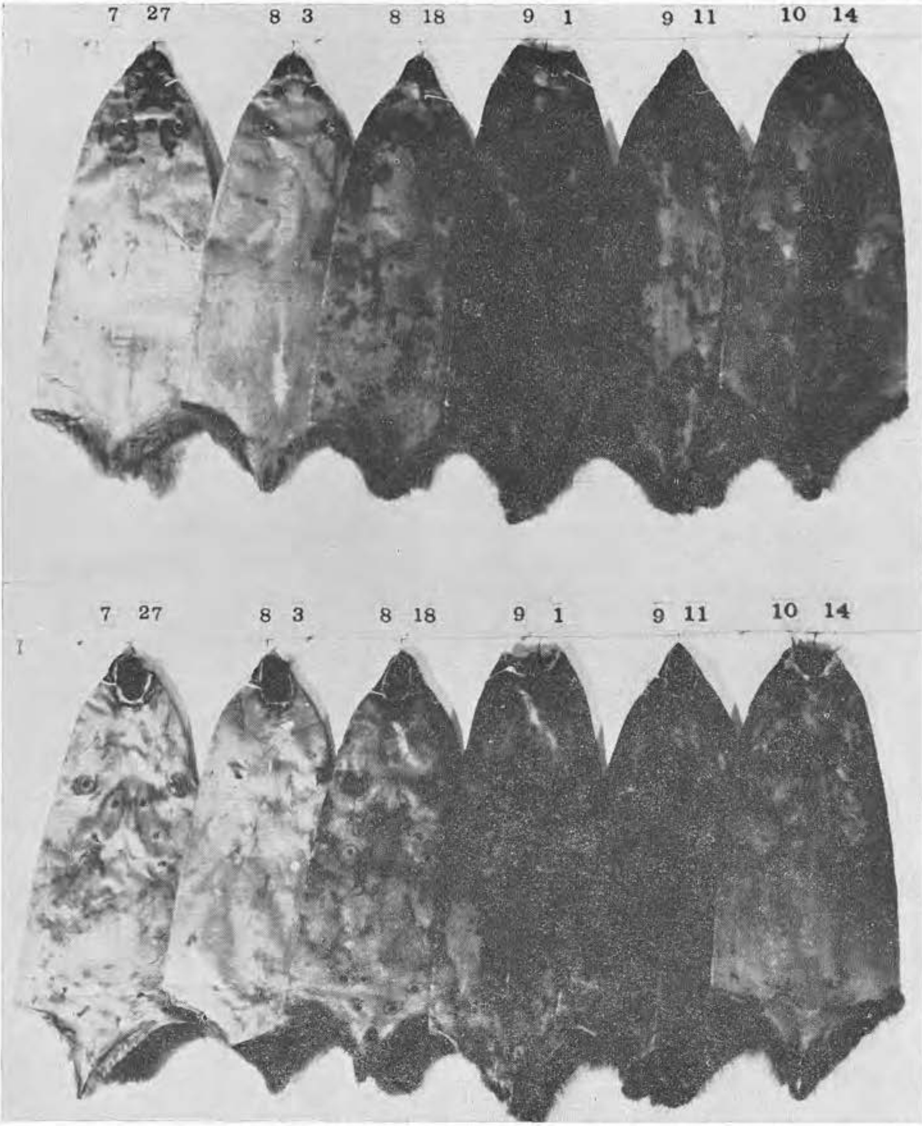


Figure 4. Dorsal (top photo) and ventral (bottom photo) views of summer adult female pelts taken in 1954.

When the ratio of young per adult for the late pelts was compared with the young per adult for each entire season it was found that the late pelts had slightly less young per adult than did the seasonal average (Table 1). While these differences are not all significant, they do suggest that late-caught muskrats were mistakenly classed as adult because of their adult-like patterns, and that these may be depressing the number of young per adult in the sample.

If this interpretation is true, then age ratios by pelt pattern obtained from muskrats taken after December

TABLE 1

Age Ratios of Late-Caught Muskrats in Relation to the Yearly Average

Winter Trapping Season	Yearly Average: Total Checked	Yearly Average: Young Per Adult Ratio	Late Muskrats Only: Dates of Check	Late Muskrats Only: Total Checked	Late Muskrats Only: Young Per Adult Ratio	Ratio Significance
1947-48	8,133	3.79	2-6-48 2-9-48	507	3.5	none
1950-51	3,259	2.2	1-29-51 1-30-51	94	1.4	at .05
1953-54	2,798	4.2	1-28-54	617	3.9	none

are unreliable and should not be used. Even though these late pelts are not completely white and can apparently still be "read", they may be biased by the presence of adult-like immature patterns. It should be reiterated here that this information is presented only in a speculative sense.

Basic Patterns. I attempted to separate the various immature pigment patterns, first on the basis of age, and then according to the month of birth, and thus set up a method for aging immature muskrats by pelt pattern. It immediately became obvious that immature pelt patterns would not lend themselves to such a separation. There was no progressive change toward a lighter pelt, nor was there one particular pattern for any one immature age group. Instead, four easily recognizable patterns seemed to recur constantly throughout all age groups. All other patterns could be considered as variations of one of these four. These "basic patterns" were designated by the Roman numerals I, II, III and IV (Fig. 5):

I. A completely dark pelt except for narrow white dorsolateral stripes which form a "lyre" on the dorsal surface.

II. A completely dark pelt except for a narrow to broad mid-dorsal stripe.

III. White belly and lateral surfaces with a narrow to broad dark mid-dorsal stripe.

IV. A completely white pelt except for two dark dorsolateral stripes forming a lyre-shaped pattern on the dorsal surface. This pattern is the reverse of a I pattern.

It is a matter of interpolation into which of these classes the many intermediate pelts are placed. These pattern designations are quite arbitrary and do not indicate any particular order or sequence, but merely give a convenient means of separation.

Clear white patterns are found in spring pelts, and under certain circumstances, at other times of the year. These we have termed "V" patterns, because they are distinct from IV (Fig. 6).

In kits less than 90 days of age, a completely dark pelt devoid of any

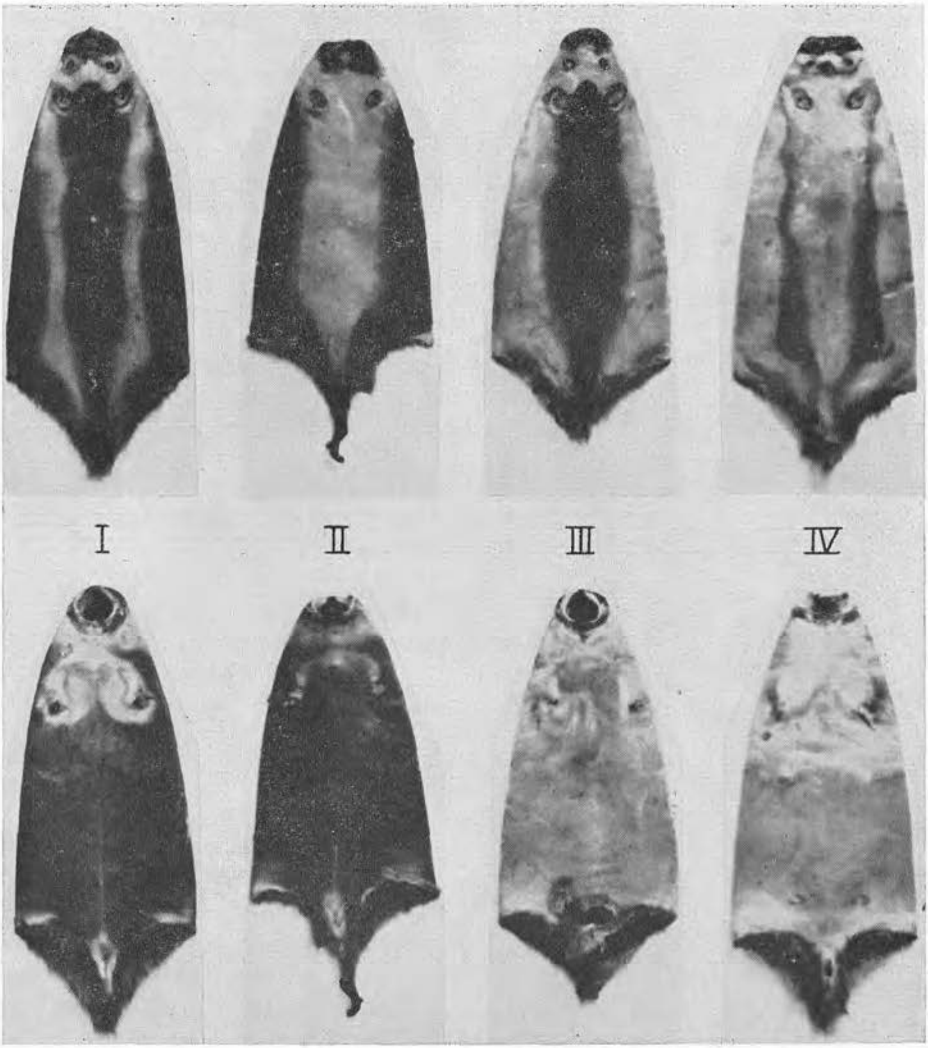


Figure 5. Dorsal (top photo) and ventral (bottom photo) views of the four basic pelt patterns for immature muskrats taken in fall and winter.

white stripe is common. This pattern is rarely found in the older immatures, but in the 1958 trapping season it showed up with surprising frequency. Habitat conditions during the summer of 1958 were unusually poor for muskrats, with extreme drought conditions prevailing. Whether this dark-phase pelt is directly associated with detrimental habitat changes is not known. However, as long as it is important in some years, we have separated it from the I pattern by the numeral "O" (Fig. 6). In terms of amount of pigmentation there is very little difference between the I and O patterns.

The relatively large number of pelts from kits of the same litter but taken individually over a period of time, were also checked. If we assume that

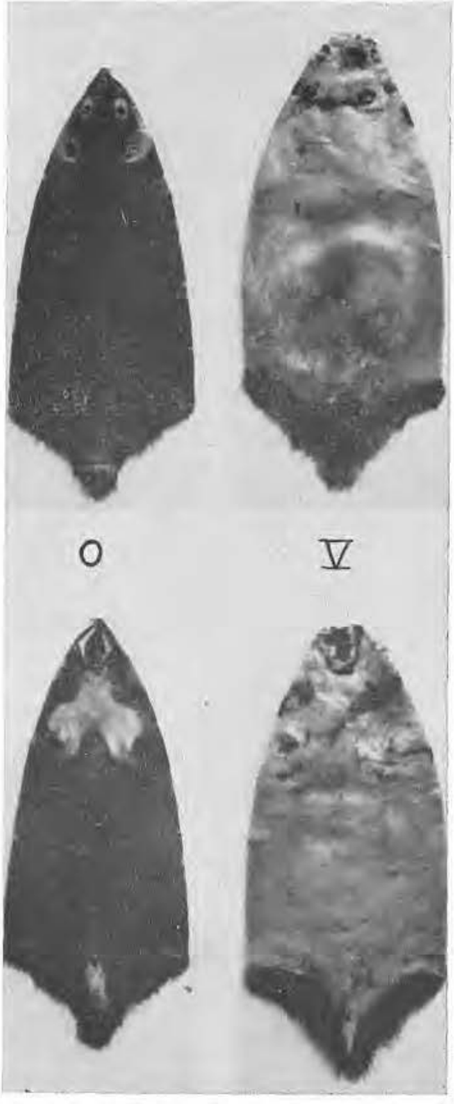


Figure 6. Dorsal (top photo) and ventral (bottom photo) views of completely dark (O) and completely light (V) immature pelt patterns found in summer and spring.

all kits in the same litter begin life with the same pattern (a III pattern, as will be shown later) then it is reasonable to expect that litter mates will progress through the same pattern phases (with some individual variations in time) as they grow to adulthood. However, we found that the patterns of these litters were not continually getting lighter as the season progressed, but seemed to fluctuate from light to dark phases and back again. For each year's collection, all known-age pelts were separated out according to the "basic patterns". The frequency of occurence of the basic patterns among all known-age fall and winter immature pelts is shown by age group in Figure 7. Ages were combined in seven-day periods. No differences were evident between years.

No one pattern is completely representative of any particular age group, although high points in Figure 7 indicate where certain patterns are more typical than others. These high points, therefore, represent the pattern that the majority of muskrats should have for that particular period. The pattern overlap more or less represents individual variations that tend to obscure the expected changes.

The most important patterns are I and IV, with 86 per cent of the total patterns exhibiting these. Patterns II and III, however, appear to be more important in the earlier age groups and there is an indication that they may increase in numbers again in the older muskrats which are reaching prime. These latter two patterns make up only a little over 13 per cent of the total known-age collection, but in the age group between 100 and 141 days, they make up 44 per cent. This is the age period which would compose the bulk of the early fall muskrats and is, therefore, of importance. It is possible that a larger sample of this age group would show a different pattern composition, but the supplementing of this

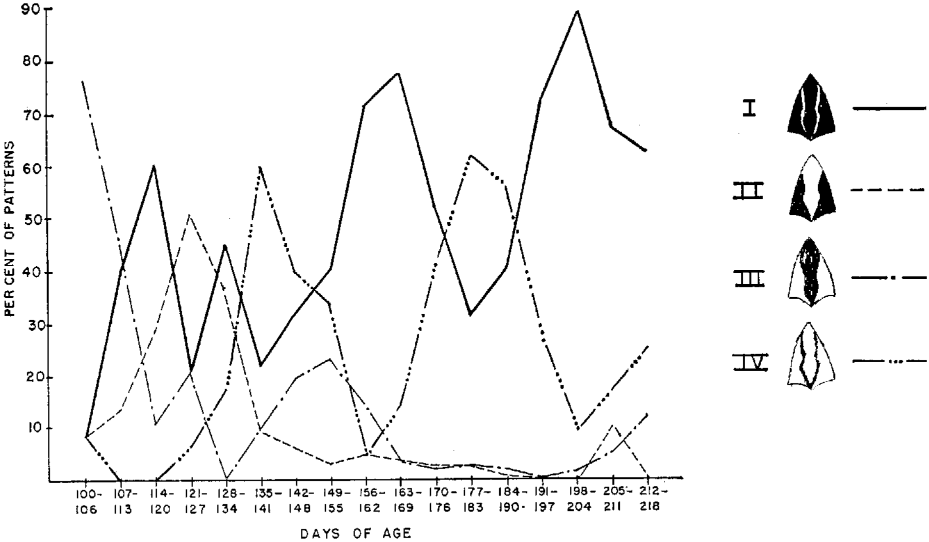


Figure 7. Periodic pattern fluctuations according to age in 868 immature muskrats. (I, 441 pelts; II, 50 pelts; III, 64 pelts; IV, 313 pelts.)

fall and winter collection with 103 immatures taken during the summers of 1954 and 1955, plus additional fall and winter pelts from 1956 to 1957, made no changes in occurrence frequencies.

Fluctuations of dark and light pattern phases are apparent in Figure 7. This correlates with pattern changes found in pelts from family groups.

Immature muskrats taken in summer were of varying ages. Very few could be aged with any degree of accuracy, but comparisons could be made concerning pattern types represented. The same basic patterns found in the fall and winter collections occurred throughout the summer collection.

Hair Growth and Pattern Development

Age 1 to 115 Days

Early hair growth and patterns were studied in 33 nestling kits during 1954 and 1955. Observations covered the period from 3 to 30 days of age.

All kits begin life with a III pattern. From birth until about 10 or 11 days of age, the pigment pattern is visible from the external surface in the living kit because of the small amout of hair coverage. We have handled hundreds of young kits during past litter-tagging operations, but we have not seen any 5-day-old kits or younger with anything but a III pattern. The pattern of this beginning stage therefore, seems reasonably well established.

Intense hair growth took place on the back of the 3-day-old kit with most of the short, incoming hairs being guard hairs (Fig. 8). At this age hairs were extremely short, probably not longer than 1 mm., and intensely black. The belly was almost hairless, with a few fine, white, scattered hairs. In the lateral regions hairs were found having the appearance of young guard hairs, but with little or no pigmentation.

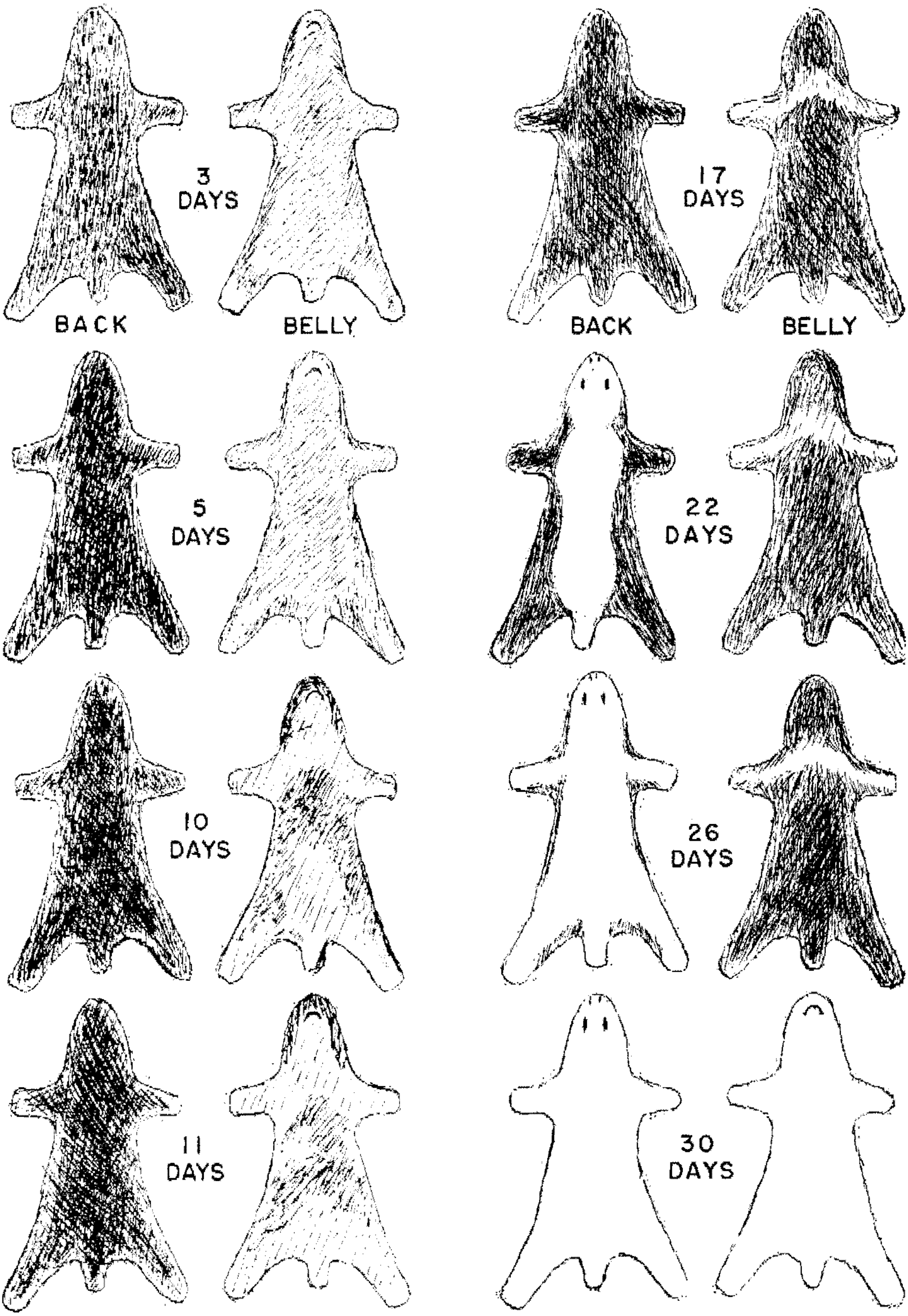


Figure 8. Diagrams of nestling kit flesh surface patterns

They were probably the colorless tips of young guard hairs. Black pigment spots were numerous in the belly region, thinning out and disappearing anterior to the posterior portions of the forelegs, and posterior to the anterior portion of the hind legs. These appeared to be guard hair pigments from newly forming guard hair into which they were observed to merge. They were not numerous enough to give color to the belly region; most could be observed only under magnification. This intense growth of dorsal guard hairs was reflected on the dorsal flesh surface of the skin by a very dark pigmentation. Ventrally, the flesh side was light colored, corresponding to the virtual lack of hair growth.

From these findings it would appear that on both the ventral and dorsal surfaces guard hairs are the first type of hair to develop.

5 *Days.* Pigment spots on the belly appeared to elongate and the dark portion of the new guard hair shafts were beginning to emerge. Because the guard hairs were still only a short distance out of the skin they lay at a very acute angle—almost parallel to the skin. Fur hair was not yet visible. Only a slight darkening of the flesh side had occurred ventrally, and dorsally the flesh side remained heavily pigmented.

7 *Days.* There was still no apparent sign of fur hair. If it was present it must have been extremely short. At any rate, it was not possible to pluck anything but guard hair for microscopic examination. There was an increased number of white hairs on the belly, and these in many cases were colorless guard hairs. They were probably the colorless tips of dark guard hairs which had not yet grown out to the dark portion. This idea was strengthened by the fact that white-tipped hairs with short dark bases were emerging from dark pigment spots. Flesh surfaces, with few changes, were pigmented similarly to the 5-day-old kit.

10 *Days.* Many dark guard hairs were emerging on the belly at 10 days of age. It was not possible to determine if fur hair was present on the belly region since none could be plucked. A darkening of the ventral flesh surfaces made it probable that fur hair was beginning to erupt. The dorsal area now had a fair number of fur hairs among the guard hair.

11 *Days.* The ventral surfaces were well covered with both dark guard hair and fur hair, except on the throat region and between the hind legs. Ventral flesh surfaces were dark except in the throat region and on the inside of the legs—the same areas showing the least amount of hair covering.

17 *Days.* The throat region was still only thinly covered at 17 days and the flesh surface in this region was still light.

22 *Days.* The kit had a good coat of fur all over and fur growth was beginning to cease in the mid-dorsal areas. Pigmentation was also disappearing in this region.

26 *Days.* The flesh surfaces were practically white in the mid-dorsal area at 26 days of age as hair production in this area ceased, but intense hair growth and accompanying pigmentation were evidenced in the belly area.

30 *Days.* By this time the young muskrat was fully furred with its first

coat and all hair production ceased. The flesh surfaces were now completely white and the hair follicles went into a short quiescent period.

From this point until 105 days of age, known-age pelt material in our collection is insufficient or lacking entirely so that it is not possible to follow pattern changes and hair growth through this period. However, shearing experiments to be described later provided additional information on the 30- to 105-day age period.

Pelt strip sections, as previously described, were made from some of the larger known-age litters (Fig. 9). By checking the hair-length line and flesh pigmentation in these sections it was possible to follow the direction and speed of growth of the hair. Litter mates in these litters were captured at different times and their hair development varied according to their age at capture.

From a known-age nestling litter tagged in 1954, seven of eight kits were re-captured at ages of 105 to 115 days of age. Figure 10 illustrates the changes taking place beginning at 105 days of age and continuing for the next 10 days. Since each of the diagrams represents a different muskrat in the litter, it is possible that individual variations have modified the true sequence somewhat. Nevertheless, it seems likely that this is a relatively good representation of such changes.

These animals offered important clues to pattern changes in summer litters. After photographing their pelts and sectioning out pelt strips, hair growth diagrams were made of each strip. The narrow inner ring represents the 1/8-inch strip of pelt on which the

Figure 9. A pelt strip photographed between glass. The concavity in the center of the hair profile is formed by a region of less dense older growth. Tips of the new growth can be seen just above the skin level in the center and gradually increasing in length outward until they reach the same length as the earlier growth.

diagram is based and indicates the condition of the flesh surface. Shaded areas in this ring are the pigmented areas on the flesh side of the pelts, as seen with the aid of a binocular dissecting microscope. Areas in this ring that are lightly shaded (dotted) have hair beginning to grow, but have not yet reached the stage where the hair is visible on the hair side. Dark areas (solid black) in the same ring indicate areas where new hairs have erupted and are visible on the hair side. The outer ring or rings represent hair length. Where two of these rings occur (one inside the other), the outer ring represents old hair growth and the usually broken inner ring indicates the latest growth of hair which has not yet attained full size.

105 *Days.* Diagram 1 in Figure 10 shows a III pattern at 105 days of age. Color of the flesh side in the top center, or mid-dorsal area, indicates that intense hair growth is occurring here. A concavity in the inner hair ring at this point shows that this hair has not reached its full length. The outer hair ring above it is mature hair of an earlier growth. Considering the flesh side (inner ring), hair is beginning to grow laterally on either side of the

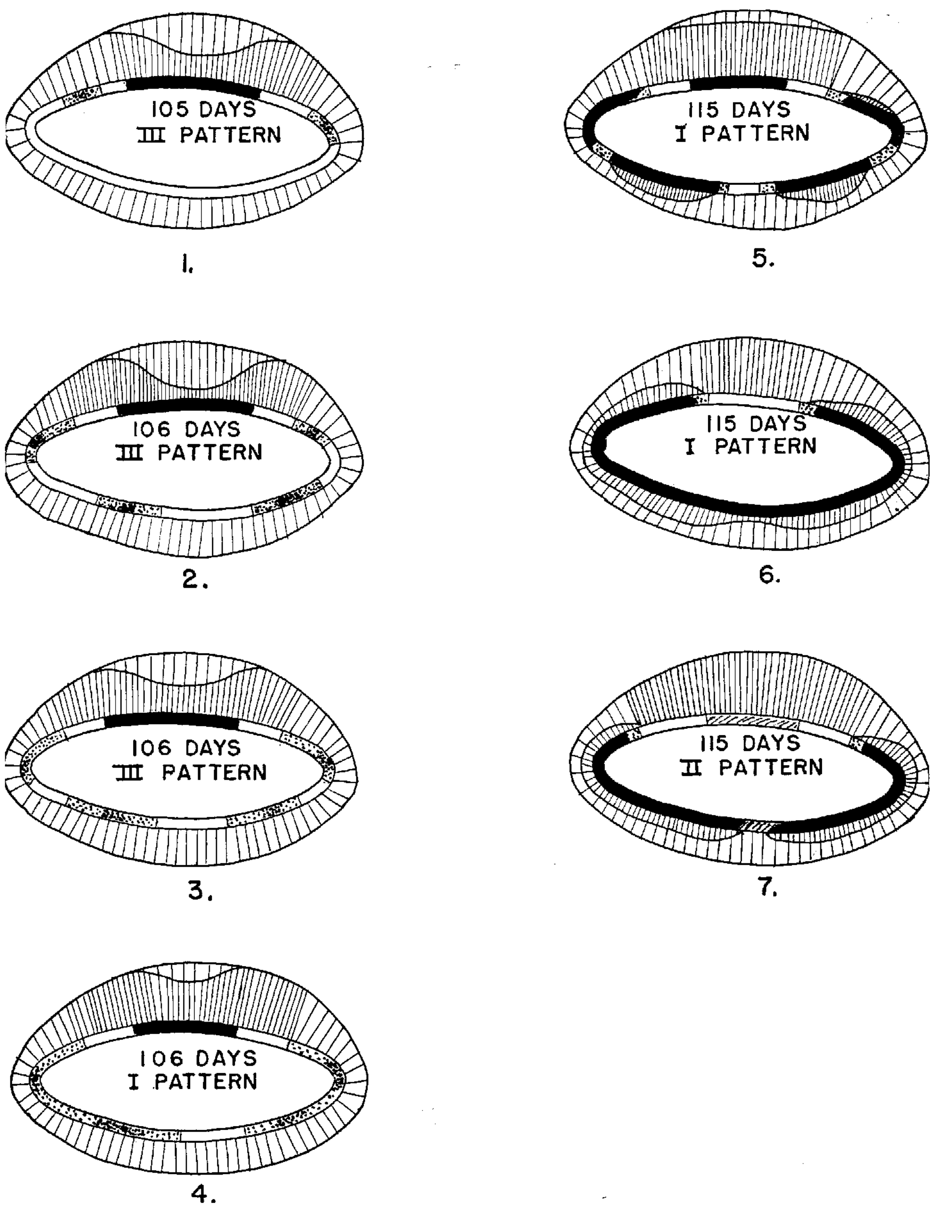


Figure 10. Sequence diagrams of hair growth in a known age summer litter of muskrats. (Strip sections around girth of pelts.)

densely pigmented center section. This growth is not yet visible on the hair side and pigmentation on the flesh side is barely discernable.

106 *Days.* In diagram 2 another III pattern is evidenced which is very similar to the first, except that new growth areas are forming in the lower or ventrolateral regions, and those in the dorsolateral regions have extended

slightly. Hair is still not evident from these new areas of growth. Diagram 3 *is similar except for an extension of the* growth areas and some growth of hair in the dorsal pigmented area. Further growth in this area can be seen in the 4th diagram; the ventrolateral and dorsolateral growth areas have coalesced on either side, leaving a light area in the mid-ventral region and two light dorsolateral stripes. Pigmentation is readily visible and the pelt pattern is now a I.

115 *Days*. Pelt diagram 5 is also a I pattern similar to diagram 4, but now hair production is becoming evident in the new growth areas, as shown by the broken inner hair rings. In the mid-dorsal region, hair growth is just about complete and the inner hair ring is barely visible. Diagrams 6 and 7 show a further extension of the inner ring to the dorsolateral and mid-ventral areas. Diagram 6 is still a I pattern. Although all pelts were sectioned about ½-inch anterior to the tail, individual variations in number 6 placed the strip through an area below the dark center stripe. This makes it appear in the diagram that the pelt pattern might be a II while actually it is a I. In diagram 7 the mid-dorsal growth is complete, and the inner and outer hair rings now coincide. Pigmentation is fading in this region and the pelt now becomes a II.

Within the same litter, pelt patterns vary for muskrats of the same age. Numbers 3 and 4 are both 106 days of age, yet one is becoming a I and the other is still a III pattern. Numbers 5 and 7 are 115 days of age, yet number 5 is a I and number 7 is beginning a II. This group of diagrams serves to illustrate the manner in which some of the pattern changes take place and makes it obvious that patterns may also change from a light phase to a dark, rather than merely becoming progressively lighter. Changes from light to dark were also recorded in three other known-age litters recaptured in summer and fall from which pelt strips and diagrams were made.

Hair growth apparently does not begin and spread from only one spot, but may originate from four or five minor growth areas. These eventually coalesce into one or two major areas, thus bringing about the pattern change. In early stages when growth areas are still separated, the new hair is not yet erupted to the point of visibility. After coalescence of the ventral and lateral growth areas, a new hair growth line begins to appear against the old hair. When dark dorsolateral stripes are present, as in the IV stage, these stripes spread toward the mid-dorsal region. The new hair in the initial stripes reach full length and dorso-lateral stripes then revert to white on the flesh side even while the mid-dorsal region is still dark and actively growing. This reversal from dark to white stripes sets the pattern up for the next pattern phase, which in this case probably will be a I.

Growth Waves

The studies on known-age dried pelts, nestling kits, and summer-trapped litters indicate that muskrat hair growth must be a series of growth waves with each wave adding to the succeeding wave rather than completely replacing it. To add further proof that waves of hair growth were occurring, we undertook a study of sheared animals using techniques described in the "Methods" section of this report. Preliminary experiments on three penned immature muskrats showed that shearing was a practical method of studying hair growth waves and that the extent of growth and the rate of filling-in could be accurately determined. By using three known-age litters in similar studies we tried to fill the gaps in our information on growth patterns between 30 and 100 days of age, and on the number of growth waves occurring between birth and the following spring.

Hair growth will be discussed here in terms of complete coverage of the body area. When a "growth cover" is said to be complete, it means that the body area has been completely filled in with a new growth of hair, but this does not necessarily mean that the new hair has ceased growing. Growth may continue for some time after the new hair has completed its coverage.

New growths are diagramatically illustrated in Figure 11 for a representative kit from one of the three litters studied. Because all kits made similar growths except for small individual differences in time of occurrence and rate of growth, results for all three litters will be considered collectively.

All ages given here are interpolated averages for the group of study kits as a whole.

2nd Growth Cover. A new wave of hair growth began around 38 days of age after about 10 days of quiescence following the completion of the "nestling" or 1st growth. In the three litters studied, all kits began their 2nd growth of hair in a similar fashion. However, while the beginning growth of the new-born kit formed mid-dorsally, the 2nd growth, in all instances observed, began on either side just posterior to the forelegs in the median lateral region of the body. Gottschang (1956) observed in *Peromyscus* that new fur appears first as a small patch or as a narrow line just above and in front of the hind leg. His observations compare well with ours on the beginning of 2nd growths.

The legs were engulfed and covered as the lateral and ventral growth wave reached them. This wave moved up to the dorsolateral region and stopped. After a short pause, growth began again, first as a line edging the inside of the mid-dorsal bare area, but later gradually spreading inward to engulf the entire mid-dorsal region. It was a very diffuse growth after its initial appearance, having no pattern of direction. Complete covering of the dorsum occurred around 61 days of age, but lengthening of the hair continued for some time thereafter, probably until 78 days of age.

3rd Growth Cover. At approximately 71 days of age, while mid-dorsal guard hairs were still growing, a new growth made its appearance once more in the region posterior to the forelegs. By 91 days of age there was incomplete coverage laterally and ventrally, but this region was completely filled in by 108 days of age. In addition, a new growth covered the dorsum, except for a nongrowing patch in the rump region. These delayed rump patches became a characteristic type of growth from this point on. By approximately 121 days of age a new growth made its appearance once more in the lateral growth centers. This was the beginning of the 4th growth wave. Simultaneous filling in of the delayed rump patch resulted

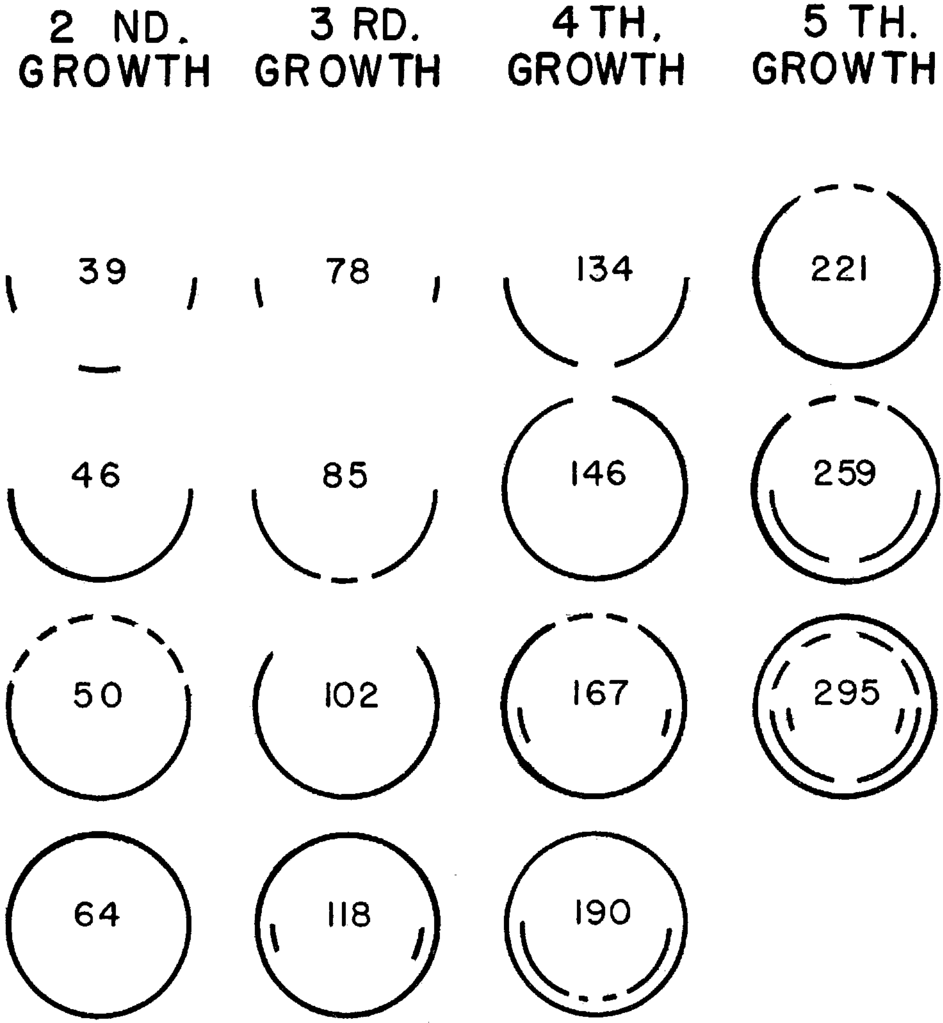
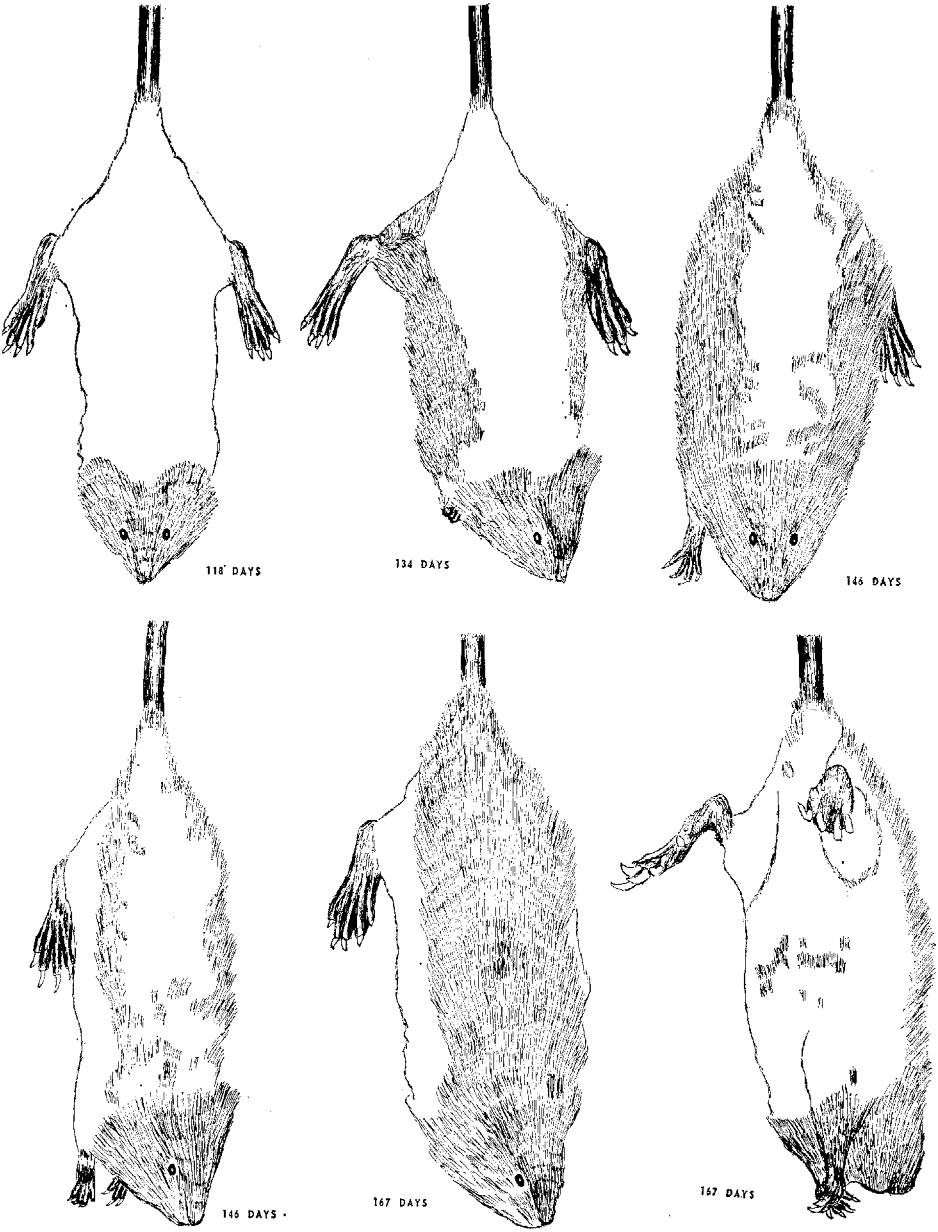


Figure 11. Growth-pattern diagrams following shearing for Kit B-519. Circles and parts of circles represent areas covered by new hair growth viewed in transverse section through the body of the muskrat. They show only extent and location of new hair coverage, not mature growths. A solid arc or complete circle indicates areas completely covered with new hair growth. A broken arc indicates growth coverage is incomplete. Concentric circles represent new growth covers forming before succeeding ones are finished. Each vertical row of diagrams indicates in number of days the time span of a single growth cover.

The sketches represent how the shearing technique was used, and show the appearance of Kit B-519 at various ages for which there are diagrams.

118 days: After complete shearing following completion of 3rd growth cover.
134 days: Development of 4th growth cover laterally.
146 days: Further growth of 4th cover.
146 days: Lateral and ventral pelage sheared, but incomplete part of 4th cover not sheared dorsally.



167 days: Dorsal view showing completed 4th growth cover, but no growth of 5th cover.

167 days: Ventral view showing beginning of 5th cover.

in completion of the 3rd growth coverage.

4th Growth Cover. Ventral growth was slow and usually failed to cover the mid-ventral area until after a delay. This delay was especially pronounced between the hind legs. At 150 days of age the delayed ventral area was still not filled in completely and the mid-dorsal stripe was just beginning to fill in. With the completion of the delayed growth area on the rump, the 4th growth completely covered the animal at approximately 178 days of age. However, the 5th growth wave was now beginning in the initial growth area behind the forelegs.

5th Growth Cover. All patterns appeared more irregular and broken, although a linear growth pattern was still evident. Rapid and smooth changes gave way to slow irregular growths. After the completion of the 4th growth or "subadult" pelage, it is probable that all further growths were intermediate to the adult type. A series of irregular patches had completely covered the animals by 215 days of age, thus completing the 5th growth. At the same time, patchy growths of the 6th cover were already well under way ventrally.

6th and 7th Growth Cover. The 6th growth cover was never completed in any of our study animals and the 7th was just begun in only one; death of the study animals terminated the observations in March. Only the oldest muskrat (295 days) had begun production of its 7th growth cover.

There were two areas of delay in pattern development, one dorsal and one ventral. The delay in dorsal hair growth first made its appearance during the 3rd growth cover. In the beginning, filling in of the dorsum occurred more or less evenly and rapidly with no obvious delay, but during the 2nd growth cover the time interval between the beginning and the completion of the growth had begun to increase. The last part of dorsum to be completed in all growth covers was an area just above the base of the tail in the rump region. With each successive growth wave this region took longer to cover, until by the 3rd growth it was out of phase with the surrounding area and there was a definite delay or break in the growth here. In later waves of growth this break amounted to 15 or more days.

The origin of the delay stemmed from the slowing down of growth in the mid-dorsal stripe. As hair growth gradually spread inward from the dorsolateral lines to fill in the center, it appeared to occur more rapidly in the more anterior parts of the stripe and gradually worked back. Just anterior to the base of the tail, in the region of the rump, hair growth failed to materialize even though the remainder of the stripe might have been filled in. This delay in growth left a small bare spot which was usually about the size of a nickel.

Ventrally, a similar delayed area developed between the hind legs. It first made its appearance one growth cover later than its dorsal counterpart. From the very beginning this area was always the last area ventrally to be completed. With each successive growth it took longer to complete, until in the 4th growth cover there was a definite delay. Surrounding ventral areas indicated new hair growth that was relatively long before new hair in the delayed area was even visible. Succeeding growth covers showed increasing delays in the completion of this area.

Other investigators have noted delayed areas in various animals. Bailey (1915) and Morejohn and Howard (1956) have recorded delayed rump patches in the pocket gopher. Collins (1923) noted delays in *Peromyscus* and cited similar findings by Jackson (1915) who worked with *Condylura.* Butterworth (1958), working with the Barrow ground squirrel, also wrote of delayed growths in the rump region.

The 4th growth covers were completed by sheared animals at varying ages. The span extended from 154 days to 221 days, or 67 days between the extremes. The average age was 192 days. This is another example of the variation of individuals in the same litter. Collins (1918) found noticeable individual variations in *Peromyscus* litters.

The 4th growth marked the approaching end of symmetrical patterns. They became more irregular, and delayed areas became numerous in all regions as adult-type growths gradually came into prominence. Generally speaking, even these adult-type growths followed in sequence the same areas as the immature growths. The belly areas were mostly completed through a series of irregular growths before the mid-dorsal region began to fill in and major growths mid-dorsally were succeeded once more by ventral growths. Because irregular adult patterns appeared to have some overlap, this description should be considered in a general sense and not as a precise manner of change.

The irregular growth, late in the spring, accompanied by comparatively light flesh surfaces indicates that there may be no period when all growth ceases completely. Instead, as the periods between growth become lengthened and the growth areas become greatly reduced in size until the flesh side of a pelt appears completely white, it may be that there are still a few inconspicuous spots of growth present somewhere on the pelt. These spots may complete their growth without enlargement and at the same time, other small spots may be forming elsewhere. With the advance of the season, when new spring growths begin to appear, these growth spots become more and more numerous and enlarge greatly in size. When hair growth has again reached maximum a large percentage of the skin is covered with dark growth areas.

Five of 12 kits showed prominent dorsal guard-hair growth when observations were made between 71 and 78 days of age after they had been sheared an average of 14 days earlier. Fur hair had lengthened somewhat after shearing, but no new growth had occurred. Guard hair, on the other hand, was abnormally long in relation to the sheared fur hair in this region. The 3rd growth cover was beginning dorsolaterally, but it does not seem likely that this dorsal guard hair growth was part of the 3rd growth cover, because dorsal growths always followed lateral and ventral growths except in nestling kits. Rather, it must have been the finish of the 2nd growth which had concluded in the mid-dorsal region in the conventional manner. Close examination of the photographic records of the animals involved showed that they had been sheared shortly after complete coverage had been attained by the 2nd growth cover, but while the mid-dorsal area was still short. The mid-dorsal guard hair growth succeeded this shearing and became quite prominent within 14 days after shearing.

No other growth followed the guard hairs until 32 days later when a normal growth, including fur hair, once again covered the dorsum. It seems likely, therefore, that this growth of guard hair was not the forerunner of a new growth, but the conclusion of a preceding one. This, of course, is a contradiction of what was found in the 3-day-old kit. Previous discussions mentioned that guard hair was the first hair to appear in the young kit and that until 10 days of age no fur hair could be detected. This would give guard hair a 10-day lead over fur hair. However, we also found in the young kit that hair growth began mid-dorsally and spread ventrally, but with the beginning of the 2nd growth cover this procedure was reversed and all hair growth began ventrally and laterally, and finished mid-dorsally. It is possible, therefore, that fur hair could also show a reversal and precede the growth of guard hair in the 2nd growth wave.

Apparently, at 61 days of age when the dorsal area was sheared, fur hair growth was ahead of the guard hair in this area – possibly guard hairs had not yet begun to grow. Consequently, after shearing, the fur hair was set back farther than was the shorter guard hair (assuming guard hair growth had started). Further growth after shearing added somewhat to the fur hair length, but because the guard hairs were absent or quite short when shearing was accomplished, they were either untouched by the shearing or else cut back very little. Because of a longer period of growth to finish, they continued to grow much longer and this gave them a dominant appearance over the closely sheared fur hairs. Microscopic checks of growth areas showed that guard hairs were still growing in an area after the fur hair no longer showed growing hairs present. However, it seems strange that these long guard hair growths were not noticed in any age group other than those of the 2nd growth cover. An explanation might be that in the older age groups guard hair and fur hair came more into phase, so that eventually both began growing at the same time. Shearing would then shorten them both. Any additional growth would be proportional, so that the lengths of both types of hair would appear normal in relation to one another.

In March, dorsal guard hair appeared to be much darker than any preceding growth of hair. Whether it was because of a darker pigment in the hair, larger diameter hair, longer hair, a greater density of guard hair at this time, or a combination of these is not known. It does seem, however, that the guard hair is longer and of greater diameter than the guard hair which preceded it in January and February, but this statement is based only on a comparison of the color-slide series of the pelages of various study animals. A more detailed investigation may reveal a different explanation.

Follicle Checks

Gunn (1932:394) stated that, "The detection of prime from unprime portions of a pelt therefore, simply requires the microscopic examination of samples of under-fur hairs cut close to the skin and an examination particularly of the root ends of these. The hair from the unprime pelt shows pigmentation of a heavy blocked type (discontinuous medulla) extending down to the cut end, while the hair from a prime pelt shows a clear hyaline structure devoid of pigmentation for a variable distance from the cut end".

To check this method, hair was both plucked and shaved from light and dark areas on a muskrat pelt and given microscopic examination. Plucking hairs from the dried pelt seemed to give better results and was less time consuming than shaving. Light areas of pelt showed all white-based hairs in accord with Gunn's findings. However, in dark areas of the pelt dark-based hairs were found; in addition, *white-based hairs in these areas still outnumbered the black.*

Further examination of the pelt with a binocular microscope revealed that hair emerged from the surface in tightly compacted groups or bundles, and that these bundles were grouped in series of three or four.

Each bundle was usually composed of varying number of fur hair — upwards to 22. These hairs all appeared to leave the skin through a common opening and were therefore considered as coming from either a single follicle or a compound follicle. Follicles with multiple hairs have been noticed by other investigators who studied various species, including man (Dry, 1926; Fraser, 1931; Wilcox, 1950). Wilcox (1950) found that the general body hair in adult chinchillas was arranged in dense clusters which contained as many as 75 hairs, and that all the hairs in each cluster emerged from a common hair pore. Although we found only 22 hairs per cluster in muskrats, a more detailed study may show that there are even more.

Gunn's (1932) illustrations of a transverse section of a muskrat skin indicated the presence of compound follicles with more than one hair emerging from a single hair pore. He made no mention of this in his writing, however. He does say that "... the underfur hair roots are arranged in groups, either around the larger roots of the guard hairs or in clusters and rows without a central guard hair" (p. 138).

In muskrats, prime or mature hair may be found in dark areas of the skin as well as in light. Thus it can be seen that within follicles some hair can be mature or prime and yet have actively growing hair associated with it.

Limited check was made of the twelve pelts selected for study, but the results are rather interesting. Five follicles were taken from the light dorsal areas and five from the dark dorsal areas on each pelt. The number of hairs in each follicle was counted and separated into either actively growing or mature hair. Hairs with a pigmented base were considered as growing hairs while clear-base hairs were classified as mature. As many as eight actively growing hairs could be obtained from a single muskrat follicle. At the same time, the number of mature hairs associated with them varied up to 14.

Younger kits tended to have less hair per follicle than did older immature muskrats. Table 2 shows that the number of hairs per follicle increased from 1 at birth to an average of 16 in

TABLE 2

Average Hairs Per Follicle in Relation to Age of the Muskrat

Age of Animal (Days)	Average Hairs Per Follicle: Follicles With All White-Based Hairs	Follicles Containing Some Dark-Based Hairs: White-Based Hairs	Dark-Based Hairs	Total	Pigment Pattern
27	1	..	..	..	V
56	5	1.7	3.7	5.4	III
160	11.6	9	4.3	13.3	I
186	10	9.8	4.4	14.2	IV
193	13.8	9.6	3.6	13.2	I
201	13.6	9.4	6.8	16.2	I
209	12.6	9.8	5	14.8	I
278*	10.4	..	..	..	O

* Runner muskrat.

the dark areas of the skin at somewhat over 200 days of age. The one exception is a runner muskrat taken in March, which averaged 10.4 hairs per follicle. This possibly was caused by abnormal stresses imposed by subnormal living conditions. The effects of stress in relation to hair growth will be discussed later.

Follicles from dark areas averaged 1.4 more hairs per follicle than the follicles from light areas. This indicates that old hairs did not immediately drop out when new hairs were produced, but were retained for varying lengths of time. As many as 14 mature hairs may be found in a single follicle accompanying up to 8 new, growing hairs. Hair shedding may not be conspicuous with such large numbers of old hairs being retained.

Inspection of a 3-day-old muskrat pelt showed only 1 hair per follicle, with the follicles relatively close together per unit of skin area. Older pelts, as stated before, showed a number of hairs per follicle with the follicles relatively far apart per unit of skin area. It would seem, therefore, that the follicles spread apart as the skin grows, but in order to maintain and increase hair density, more hair must be produced per individual follicle.

Table 3 lends some evidence to support these ideas. Follicle counts per unit of area (unit area was estimated with an ocular micrometer on a dissecting microscope) varied from 24 follicles at 3 days of age to 14 at 29 days, thus showing that follicles were continually spreading apart with growth, probably without the formation of new ones. By 56 days of age, or thereabouts, the number of follicles per unit area dropped to 5 and from there on remained relatively constant. Table 3 also shows that the length of the pelage increased until probably about 180 days of age and from then on remained approximately the same.

From age 12 to 29 days, on both

back and belly, the fur increased in length as the nestling pelage grew to maturity (Table 3). Beyond approximately 56 days of age, maximum pelage length changed relatively little and then only very slowly. At 180 days of age the maximum pelage length reached the adult range for the summer period.

Adult hair measurements from summer and fall muskrats were taken for comparative purposes (Table 4). From early August until early November, relatively little difference in maximum pelage of the dorsum could be detected. Differences observed can probably be attributed to individual variations, as the progression toward longer fur did not appear to be occurring, although the quality of the pelt did appear to improve.

Collins (1918), working with *Peromyscus*, and Butcher (1951) experimenting with the gray rabbit, have both indicated that hair growth is stimulated by plucking.

Hair was plucked from a small patch on the rump of sheared muskrat kits B-509, B-512, and B-523. On kit B-513 a spot was plucked on the belly to determine if hair could be induced to grow out of phase with the surrounding area. Muskrat kit B-512 was plucked September 23 at 78 days of age and was checked again after 32 days on October 25; no observations were made between these dates. By October 25 the entire dorsum was covered with the next growth wave. It could not be determined, therefore, whether the plucked area had caused the initial growth or not.

On January 8, at 184 days of age, these four muskrats again had small

TABLE 3

Hair Growth in Muskrats of Various Ages

Actual Age (Days)	Ventral Length (Mm.)*		Dorsal Length (Mm.)*		Follicle Count Per Unit Area
	Guard Hair	Fur Hair	Guard Hair	Fur Hair	
12	4	2	10	3	24
14	.	2	6	2	16
20	12	7	21	8	18
22	13	8	25	8	14
23	15	10	25	10	14
56**	18	11	27	12	6
151	21	11	32	17	5
160	22	11	34	15	7
179	22	14	36	18	5
180	24	13	40	19	4
186	22	14	37	20	6
193	23	12	40	18	5
201	23	11	40	22	5
209	22	13	42	18	5

* Based on maximum pelage length and not on measurements of individual hairs.

** Estimated age.

TABLE 4

Adult Muskrat Hair-Length Measurements Taken from Pelts Collected During Summer and Fall

	Date	Dorsal Guard Hair (Mm.)	Dorsal Fur Hair (Mm.)
Aug.	9	39	18
	12	40	18
	17	33	18
	24	44	17
	31	41	16
Sept.	1	36	14
	8	30	13
	14	42	18
	16	35	14
	23	35	17
Oct.	6	40	15
Nov.	8	40	18

patches plucked after first being sheared. By this time hair growth was relatively slow and sparse. On February 13 at 221 days of age the animals were checked; B-512 had grown hair on the dorsal area but only in a small spot located exactly where hair had previously been plucked (Fig. 12). The growth was definitely due to the plucking. B-513 showed a patch of hair growth covering the previously plucked area on the belly, but larger than the original plucked area. Plucking may have been the stimulus for this growth even though it eventually grew beyond the bounds of the plucked region. B-509 had experienced irregular growths dorsally. A small patch of growth covered the plucked area and other patches were adjacent to it interspersed with nongrowing areas. How much effect the plucking had was hard to determine, although it is likely that it was the direct cause for the growth covering it. B-523 exhibited a nongrowing mid-dorsal stripe with several scattered spots of growth. Whether any of these are directly attributable to the plucking is not certain.

Our results lead us to conclude that hair growth can be initiated through the stimulus of plucking even in areas that are out of phase with normal hair growth.

Shedding and Molt Lines

Shedding in muskrats is a somewhat intangible process. Unlike the situation in many animals in which definite molt lines spread progressively across the body, muskrat hair replacement takes place in a more diffuse manner. The lack of a clear-cut molt line is probably due to the density of muskrat fur. It has already been pointed out that these animals may attain a hair density of at least 22 hairs per follicle and that as many as 8 hairs may be actively growing in a follicle at one time. It seems reasonable to suppose that these hairs will not all be shed at once but rather in the order in which they were acquired. Therefore, there will always be a considerable amount of hair coverage, even during periods of increased shedding. The hair that is retained will tend to mask molt lines.

Molt lines are present to a limited extent in certain age groups at particular times, but they are seldom clear cut. Some immature live-trapped animals taken from the latter part of August through early fall had somewhat shorter hairs in the mid-dorsal stripe. The flesh side of such pelts exhibited a III pattern, or some variation

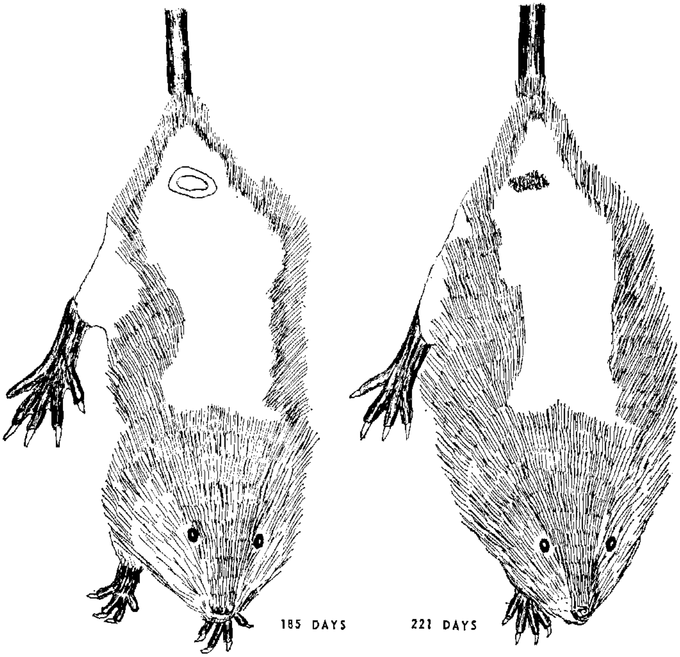


Figure 12. Kit B-512 showing effect of plucking in a sheared area. Plucked spot on rump at 185 days is bounded by a ring of white paint. At 221 days of age, only the plucked area showed new growth in the mid-dorsal stripe.

showing a darkly pigmented center stripe. In most cases this area of shorter hair could be observed only when examined closely. Guard hair in this region came away easily when pulled. These animals were estimated to be 100-105 days of age. Younger muskrats apparently did not show this area of differential hair length, as it had never been observed in small kits.

Between November 1 and 18, two litters of caged muskrats shed a noticeable amount of hair. At the time of shedding the youngest of these litters was 134 days and the oldest was 146 days. Sheared-kit data indicated that at about this age the muskrat was attaining its fourth or subadult pelage. It would seem logical to assume that this fall molt in immatures is based on age rather than time of year, considering that immature growths appear to be closely correlated with age. If this is the case, the logical time for a molt to occur is when the character of the fur is changing to become more adult-like in color and texture.

Shedding, or molt, was gradual and more or less diffuse, with the exception that it was possible in some animals to note a difference in length between the mid-dorsal growing area and the nongrowing lateral areas. This difference was not pronounced, but could be observed if closely examined. This was the only period of shedding that had been observed during the course of development of the immature pelages from birth to adult. Perhaps the change in subadult pelage resulted in a more drastic and noticeable change in the character of the fur than occurred in subsequent pelage growth, and this produced a more

TABLE 5

Body Weights in Ounces of Penned and Wild Muskrat Kits

	Penned			Wild*		
Age in Days	Male	Female	M & F	Male	Female	M & F
30-39	10	9	10	8	6	7
40-49	10	11	10	9	10	10
50-59	..	14	14	13	13	13
60-69	14	16	15	13	12	13
70-79	18	18	18	20	18	19
80-89	19	..	19	19	18	19
Mean, 30-89 days			15			14
90-99	21	20	21	23	22	23
100-109	21	22	22	28	25	27
110-119	24	22	23	30	29	30
120-129	..	22	22	28	29	29
130-139	25	24	25	32	28	30
140-149	24	..	24	33	31	32
150-159	..	23	23	36	35	36
160-169	24	..	24	37	36	37
170-179	..	24	24	37	34	36
180-189	22	22	22	38	37	38
190-199	27	..	27	39	38	39
Mean, 90-199 days			23			32
200-209	..	24	24			
210-219	22	22	22			
220-229	26	25	26			
240-249	..	27	27			
250-259	27	25	26			
260-269	..	24	24			
280-289	30	29	30			
290-299	31	30	31			
Mean, 200-299 days			26			

* From Dorney and Rusch (1953)

definite line of demarcation between the two growths.

Shedding occurred in caged adult muskrats both in spring and fall, but there was no evidence of hair sloughing off in patches and leaving bare or almost bare areas, as occurs in other species. An adult muskrat was live-trapped on September 1 that showed patchy shedding. Guard hair came out very easily in many places. Along the rump and hips underfur was very short and guard hair was scanty. Molt patches followed the typical adult irregular patterns.

A pair of adults that was being held showed an increase in shed hair on September 3, thus correlating in time of molt with the live-trapped animal. However, during the previous season, the male of this pair shed quantities of hair on November 8, so it would appear that there may be considerable variability in the time of adult shedding.

Three different groups of animals that were immature during the previous summer shed hair in quantity during the middle of March while they were being held in cages. On the other hand, a pair of animals that were already adults during the previous summer shed hair during the first part of May, although some shedding had been noted earlier. Perhaps adults of two or more years tend to shed later than young adults from the previous season. However, the small number of animals involved precludes making any conclusions on this matter. In general, the inference from these observations is that adult muskrats shed hair in quantity in the spring of the year and again in the fall. Gradual shedding by both adults and immatures occurs throughout the year.

Factors Affecting Hair Growth

Body Weight

Our hair-growth studies confirmed the statements of Butcher (1939), Baker (1951), Strangeways (1933a), Durward and Rudall (1946), and others that physical condition and certain forms of physical stress have a modifying influence on hair growth and pigment patterns.

Three of the muskrat litters used in our studies were born of captive wild parents, while a fourth litter was captured in the wild at about 22 days of age. Regardless of their parentage, these litters showed similar patterns of growth except for minor individual variations. While all four litters appeared healthy and vigorous, after they reached 90 days of age they became progressively more underweight for their ages. Table 5 shows a comparison of average body weights of the study litters with weights of wild litters from Horicon muskrats found by Dorney and Rusch (1953).

Our study muskrats were small, but not to the point of weakness or emaciation. They ate well and were active. A supply of food and water was present at all times and whenever possible natural foods were provided. In the fall and winter months when natural foods were difficult to obtain they were gradually shifted to a diet of prepared rabbit checkers, corn, and apples. It was mainly during this period that penned kits failed to gain weight at the same rate as the wild kits.

Whether there is a direct relationship between abnormally low weights and the discontinuance of natural foods is a matter of conjecture, but a dietary deficiency does seem to be indicated regardless of the cause. What effect this had on hair production is also uncertain, but we believe that the general sequence of pattern changes probably did not change, even though there may have been a shift in time of occurrence and length of hair growth periods.

Kits B-523 and B-508 of the pen-raised litters were recorded as being 1 ounce and 2 ounces lighter respectively than their litter mates at 33 days of age. At this time they had just completed their 1st growth cover. In relation to their small size, the difference in weight was important at this early age. While the rest of the kits began showing a new hair growth at 38 days of age, B-523 indicated the beginning of new hair growth at 47 days of age and B-508 at 44 to 46 days of age.

All kits had a full coverage of 2nd growth hair by 61 days of age, but while it consisted of all long hair in the heavier kits, the two light ones showed only short incomplete hair growth, indicating they were still behind in hair development. Weight differences gradually decreased with age, but B-508 remained slow in hair development. While some of the other animals in this litter began their 6th cover, B-508 never completed its 5th in the same time period. However, regardless of the number of growth covers completed, all kits showed the same type of development; differences were merely a matter of speed in development. All sheared litters are comparable in this respect.

I assumed that sheared kits showed near-normal development patterns, but due to physical underdevelopment their required hair growth periods may have been lengthened; consequently, wild muskrats may complete more growth covers than the penned animals do. It is possible that wild muskrats normally complete seven growth covers, as there was one wild kit that started its seventh, and that the time required for completion is considerably shorter. Most wild muskrats may finish their seventh growth cover in January and February. It also may be that the later hair growth covers, under normal conditions, are less irregular than those found in the shearing studies.

Diet

There seems to be a correlation between hair production and diet in muskrats. During severe winters when the water on Horicon Marsh freezes to the bottom, the amount of food available becomes less and less until finally muskrats are forced to leave their home territory and seek food elsewhere. Usually this results in their chewing out of their lodges and wandering about on top of the ice where most of them eventually succumb to cold and starvation. These wandering muskrats are termed "runners" by trappers, who sometimes pick them up in fairly large numbers during especially cold winters. Examination of pelts taken from such animals reveals that they mostly bear IV and V patterns, indicating little or no hair growth taking place; yet the skin is thin and papery. Fur buyers are not eager to obtain such furs because the thin skin makes fur preparation difficult.

During the summer and fall of 1955 a number of muskrats were held in pens for varying lengths of time. The principal part of their diet was apples. Six of these muskrats were pelted after an average of about 22 days confinement. All showed minimum hair production, a IV pattern, and the same general appearance as the muskrats previously discussed. As might be expected, this indicates that not only quantity, but also quality of food is important for good hair growth. These muskrats had been held for periods ranging from 19 to 28 days before pelting.

Four other muskrats (Fig. 13) died while being held in pens on a similar diet. Death occurred in one of these animals (No. 29 in Fig. 13) after only three days of captivity. Its pelt revealed a II pattern.

The remaining three of this group lived from 60 to 72 days after their

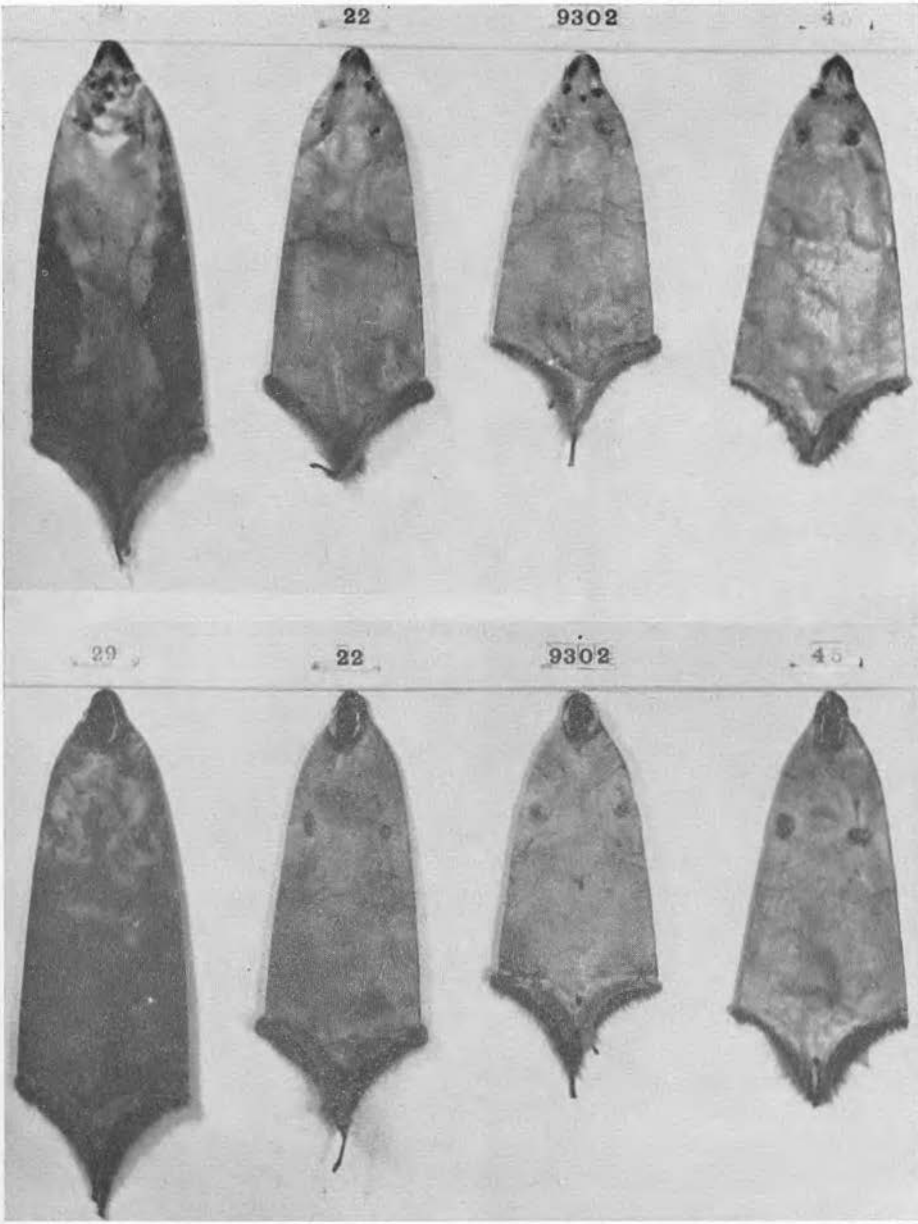


Figure 13. Dorsal (top photo) and ventral (bottom photo) views of four muskrats which died in holding pens.

capture. They all showed completely white V patterns upon skinning, indicating no hair growth taking place. No autopsies were performed on these animals, but it was assumed that dietary deficiences were probably the cause of death. Whatever the cause, however, the possibility is indicated that prolonged illness may result in the complete stoppage of hair production sometime before death. This would account for some of the clear white skins with rather poor pelage that are sometimes found in early pelt collections.

The lighter-weight pelts are probably from animals that have been subjected to stress. If hair production ceases under stress, then it is to be expected that collections of pelts with light-colored flesh surfaces will have a higher percentage of thin-skinned pelts than collections containing dark pelts with actively growing hair. Our observations on the relationship of health and hair growth are more or less in agreement with the findings of Dieke (1947), Kellogg (1947), Strangeways (1933b) and Lavrov (1944).

A white flesh side of pelts from unthrifty muskrats is not necessarily indicative of a prime condition, but rather that hair production has ceased. A pelt of this type may have an almost pure white pattern and yet be very thinly furred. It would seem that when the normal requirements for food are no longer met, the animal ceases to produce fur and uses up food reserves that have been stored in the dermis, thus cutting down on dermal thickness.

Other investigators have attempted to correlate dietary intake with hair production. Lightbody and Lewis (1929) stated that hair production in the albino rat was related to the protein and cystine content of the diet, but the demands for protein and cystine for the growth of hair appeared to be secondary in importance to the demands for growth of more essential body tissues. Butcher (1939) noted similar effects. Our observations tie in with the idea that preceding and during starvation periods hair growth slows down and eventually ceases. Accordingly, metabolism must be concentrated on keeping the muskrat alive at the expense of such secondary body functions as growing hair.

Pregnancy and Parturition

In our summer muskrat collections, adult males showed only a moderate increase in pigmentation from spring until September. Adult females, however, revealed moderate spring and early summer pigmentation followed by a pure white pelt in late July and early August. This in turn, was replaced by very intensely pigmented pelts in September.

Strangeways (1933b) found that in the guinea pig hair production decreased during pregnancy and practically ceased from parturition until two weeks afterward. Collins (1923) noted that hair growth ceased for about four weeks after parturition in *Peromyscus*. Our collection of females seems to be indicative of a similar situation.

The very light pelts may be those of lactating females with a litter. After about thirty days when the young are weaned the female begins to produce hair once again. The pelt shows unusually intense pigmentation because more than the normal amount of hair is being produced to make up for the period when there was no production. Gradually this heavy growth tapers off and the muskrat gets back to normal.

The build-up to winter fur after spring shedding is relatively slow and even in adult males. Unlike the female, males have no interruptions in hair production during the summer, so

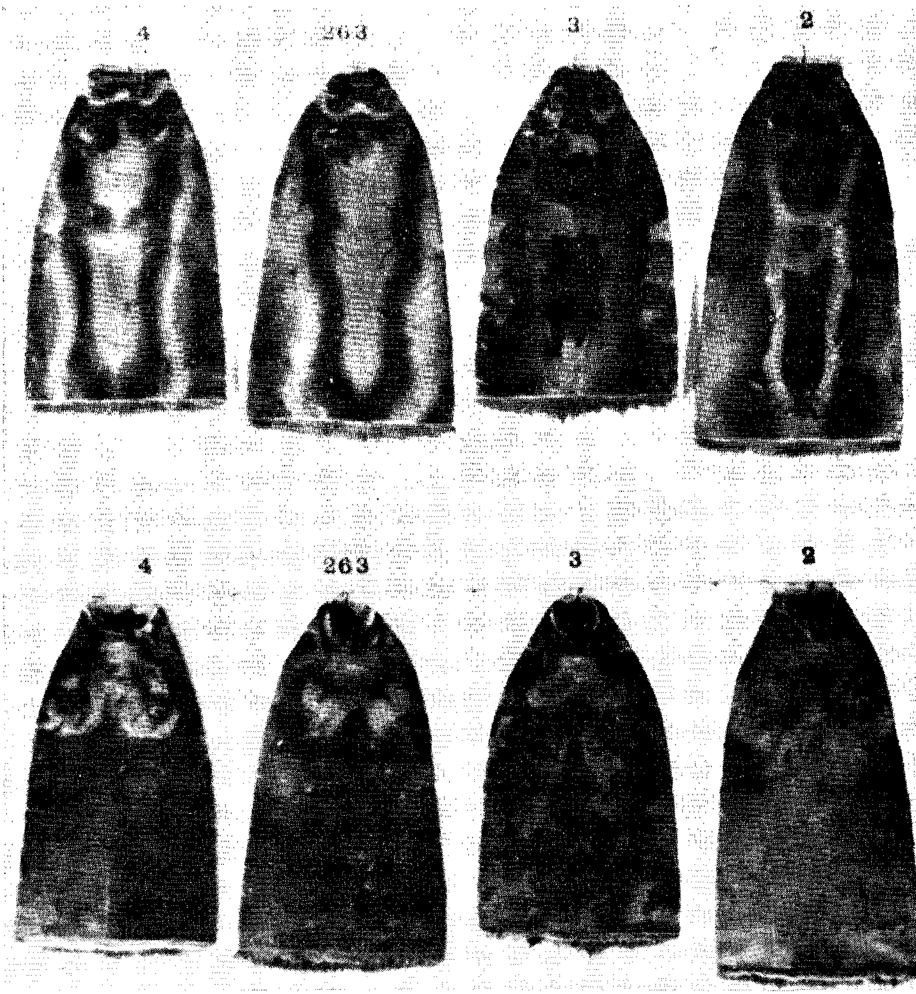


Figure 14. Dorsal (top photo) and ventral (bottom photo) views of dried pelts from a known-age litter trapped in November. Note the adult pattern of number 3.

pigmentation and hair production do not intensively increase for even a short period in the fall. Hair growth in the male is probably a continuing process throughout the year except for the spring prime period.

An *immature* female carrying seven embryos was taken in the same summer that she was born; she showed a II pattern. The explanation for the dark pattern in this case is probably that the stoppage of hair production occurred with parturition and lactation. This animal was taken on July 27 and could not have been more than 90 or 95 days of age. When the early-born females on Horicon Marsh breed at such an early age, they still have ample time to return to normal patterns again by November.

An *immature* muskrat that showed signs of breeding had an adult pattern when taken in the November trapping season (Fig. 14). This is an unusual case, as we have not found any other instances of known-age immatures bearing adult patterns. It may be that the causative agent was the stress of pregnancy and parturition.

Injury

When handling a large number of pelts, abnormalities in patterns are found. Close examination sometimes reveals that these pattern defects are associated with past injuries to the pelt. Scars from wounds may show increased hair growth around the edges. If these occur in what should be a light area, it will result in a dark spot. Strangeways (1933b) found that injuries also caused abnormal hair growth in guinea pigs.

Weather

While we made no specific study of the role of weather in relation to hair growth, our observations indicate that weather is of minor importance under normal circumstances. Had this not been true we would have been unable to combine pattern data for the various years without significantly distorting Figure 7. Gottschang (1956) and Goin (1943) working with *Peromyscus,* Hamilton and Cook (1946) working with muskrats, Hadwen (1929) and Morejohn and Howard (1956) working with pocket gophers, all concur in this view.

Weather affects hair growth mostly in an indirect manner in the form of imposed stresses. If a muskrat is forced from its home during a severe winter because of a food shortage caused by thick ice, the animal will be subjected to the stresses of starvation and unaccustomed cold. If it manages to survive for any length of time under these abnormal conditions, hair growth will all but cease.

Because only extreme temperatures causing severe hardship to the animal result in noticeable changes in hair growth, we believe that warm temperatures imposed upon our penned animals had little effect on their hair growth.

Experimental Shearing

Since normal temperatures within the extremes usually encountered by a muskrat have little or no effect on hair growth, the removal of body hair by experimental shearing should have no effect when the animal is confined in a building with temperatures maintained between 60° and 80° F. There can be no mechanical stimulus produced by shearing which would cause hair to grow, because the outer hair shaft is not a living structure which could be stimulated by cutting.

Unlike shaving, which could conceivably irritate the skin and thus stimulate growth, shearing is nonirritating. Butcher (1951) said even shaving has no such effect. Strangeways (1933a) experimented with the effects of shaving on guinea pigs and found increased amounts of hair being produced after repeated shavings. Dieke (1947) working with black rats, found that clipping hair did not stimulate new hair growth.

Judging by the findings of these workers and our own observations on penned muskrats, if shearing does have any effect on the time of replacement of normal growths, the effects are so small as to be of little consequence.

DISCUSSION AND CONCLUSIONS

Dating Pelts by Color

During the course of this work I have had numerous contacts with fur buyers, many of whom have intimated that they could tell the time a muskrat pelt was taken. I have on occasion tested them. Under the share-trapping system at Horicon Marsh, the fur is divided with the trapper at intervals during the season whenever the total catch is large enough to warrant a division. Pelts selected from various divisions have occasionally been shown to fur buyers and they were requested to state the division period in which they thought these pelts were trapped. In general, their estimates were considerably less than accurate. One of our leading fur buyers was asked to state the dates on which he thought pelts from one of the known-age summer-trapped litters were taken. His estimates varied from October through the first of November. He expressed extreme surprise when told that all these animals were taken from August 17 through August 27.

A fur grader who was hired by the State to grade its share of the fur on several occasions stated that he believed that some of the trappers were cheating by slipping in pelts of poorer quality from other divisions. He based his opinion solely on the color of the flesh side of the pelt and roughly described changes he expected to take place in the pelts as the season progressed. He did not distinguish between blotchy adult patterns and the symmetrical immature patterns which exhibit a different type of pattern development. Because of such complicating factors as repetition of immature patterns at various ages, pattern overlap, individual variation, and extremely gradual adult pattern changes, it is virtually impossible to determine the time of year a pelt was taken by the color of the flesh side alone.

Growth Wave Concepts

The findings reported here indicate that priming takes place as a succession of waves of hair growth and that the skin changes from dark to light and back again a number of times before the pelage really becomes prime. Pattern changes with time are not progressive in one direction, but show an alternation of "growing" and "resting" phases, or dark patterns to light and back again.

Kits showed an intense growth of hair in the dorsal region beginning at birth, which spread over the entire pelt by 19 days of age and then receded to a complete absence of growth at 28-30 days of age. Older kits again showed pigmentation and active growing patterns, indicating that a second period of growth must have followed. It seems logical that these periods of follicular activity be termed "growth waves."

Pelts taken during summer were from animals of various ages, but only in very few cases was the actual age known. However, it became apparent when IV patterns were found in late summer in relatively small immatures that this "resting" pattern could not possibly be the final stage before complete prime. More hair growth had to take place if the winter pelage was to be attained. Therefore, a dark "growing" pattern necessarily had to follow and would, of course, constitute another "wave" of hair growth.

Many known-age litters were recovered wholly or in part during fall trapping seasons. Individual members of these family groups were often taken over a period of time. Because of the variations in age at capture, their collective pelt patterns were indicative of the change taking place with age. They revealed that "growing" patterns are not limited to ages preceding a "resting" pattern, but may occur after phases of little follicular activity as well. This further increases the validity of the proposal that "waves" of hair growth are occurring.

Follicular checks revealed that two to three times as many mature hairs as growing hairs were found in follicles located in dark, growing areas of the skin. Hair replacement must therefore be a continuing process over a long period of time. As a hair reaches full length, matures, and becomes white-based, another hair is being produced in the same follicle to eventually replace it. Mature hairs are retained for varying lengths of time so that it is common in older muskrats to find four or five new dark-based hairs in a follicle with a dozen mature hairs. In areas with a pure white flesh side, all hair is mature and follicles are in a quiescent state. The fact that two to three times as many mature hairs as growing hairs exist in a follicle would seem to indicate that previous waves of growth had occurred to build up this number.

Through the shearing of captive muskrats, up to 7 growths from birth to the following spring have been identified. Each growth area as it completes its growth is succeeded by a short period of rest. The findings from this phase of the study substantiated the indications in the preliminary growth-pattern studies (Fig. 7) that there are alternating growth and rest periods producing waves of hair growth. Also the process of primeness in muskrats is not a simple matter of new hair growth in the fall of the year which continues uninterrupted toward eventual prime in the spring, as past literature has indicated.

The theory that hair growth occurs in waves is not really a new concept, as workers in other fields have written about the occurrence of "waves of hair growth" in other rodents as early as 1911 (Bailey, 1915; Collins, 1923; Dry, 1928; Dawson, 1930; Butcher, 1934; Haddow *et al.*, 1945; Baker, 1951). What is new is the application of this theory of hair growth and primeness in muskrats.

The idea that hair density is gradually increasing conforms with Lavrov's (1944) finding that there is an increase in pelage density until a muskrat becomes prime in the spring. The repetition of patterns accompanying such waves of hair growth could account for the difficulties encountered in attempting to age immature muskrats by pigment pattern.

Correlation and Timing of Pattern Changes

A general sequence of pattern change giving *expected* patterns for any particular age period can be synthesized. This does not mean that all muskrats during a particular period will have a certain pattern, but during that period more muskrats will have the pattern than will not have it. These pattern changes are based on *age* of the individual muskrats that make it up and *not on the time of year*. Therefore, it does not in any way indicate expected pattern changes for muskrats of unknown ages. Age, rather than time of the year, appears to be the major pattern-determining factor in immature muskrats. Time of the year is important only indirectly, in that it determines the age of the muskrat.

A sequence of expected changes constructed from Figure 7 is shown in Figure 15. A pattern is considered dominant for a particular age group when its percentage rises above the percentage for the other three patterns in Figure 7, and the extent of its dominance is equal to the period for which its percentage exceeds the other three patterns. It would appear that there is no rhythmical order to the changes below 134 days of age. However, in considering the four basic patterns in terms of follicular activity, more than 50 per cent of the follicles are in production in any particular I pattern. In a II pattern, although there is less follicular activity, it is still above 50 per cent. A III pattern indicates less than 50 per cent of the follicles are active, and a IV pattern shows considerably less than 50 per cent activity. Thus it is possible to combine the four patterns into two groups; those with more than 50 per cent follicular activity and those with less than 50 per cent activity. For ease in understanding, the former group will be termed "growing" and the latter "resting" patterns.

Figure 15 shows on the basis of "growing" and "resting" patterns that the period between 111 and 135 days of age is dominated by three growing patterns. Combining the spans of their dominance yields a period of growing patterns for 24 days. This is followed by a resting pattern for 14 days during the period from 135 through 149 days of age. The pattern becomes active again between 149 and 175 days for another 26 days, and is resting between 175 and 189 days for 14 days. The final phase between 189 and 218 days of age is active and extends for 30 days, but because our sample size drops off to nothing at the end of this age group the extent of the span is uncertain. The beginning resting pattern between 100 and 111 days is also based on incomplete figures because our sample did not include pelts from animals below 100 days of age. Figure 15 indicates, however, that both these patterns could be expected to cover a greater span.

Resting patterns of approximately 14 days duration alternate with growing patterns averaging 27 days in duration and these changes are very definitely of a rhythmical nature. In other words, an animal increases hair production until its pattern changes to one where more than half of the total area of the pelt has active follicles. Hair production continues until all the pelt has active follicles. Few fall muskrats will ever attain this maximum activity because some small areas usually remain out of phase with the

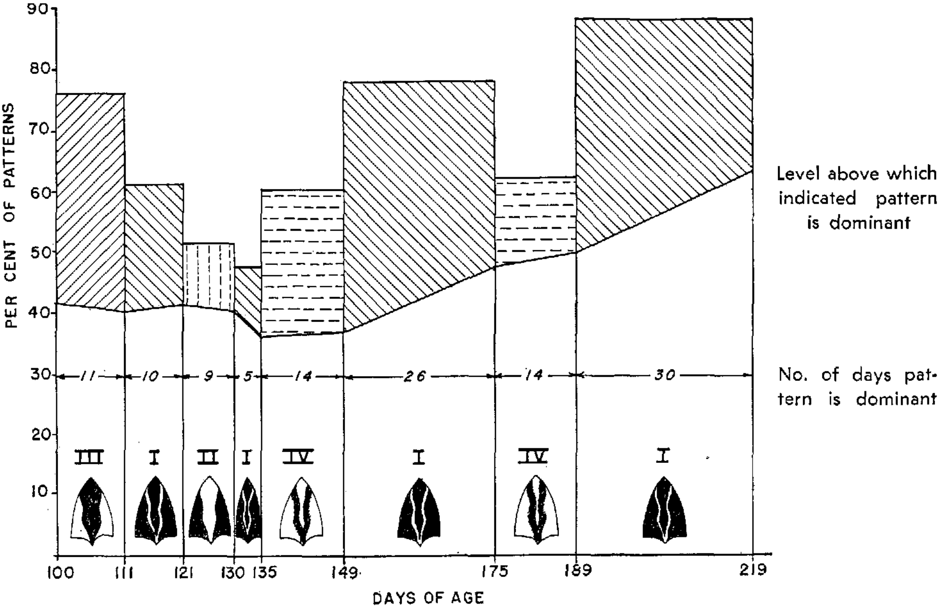


Figure 15. Pattern dominance by age period based on pelt patterns.

main area. After the point of maximum hair production is attained, hair growth gradually decreases until a minimum of growth is taking place. Minimum growths usually do not drop off to zero, again because of small areas that are growing out of phase with the main area.

We can speculate on the reason for the quick alternation of patterns in early age groups. As previously stated, II and III patterns are found in greater numbers in these early age groups. Starting with a III pattern (Fig. 15), all follicles except those in the mid-dorsal stripe are in a quiescent state. The succeeding pattern is a I, with intense hair growth occurring everywhere except for the narrow dorsolateral stripes. If this I succeeded the III, then indications are that hair growth continued in the mid-dorsal area even after a wave of growth had covered the ventral and lateral areas with pigmentation up to the dark dorsal stripe (Fig. 16).

Some imperceptible barrier stops the ventral and lateral growth wave short of the still actively producing mid-dorsal area, and the dorsolateral stripe is thus formed for the I pattern which has been produced. The next pattern is a II, showing that hair production in the mid-dorsal area has finally ceased, but that the lateral and ventral regions are still active. This is succeeded by a I pattern once more, but only for a brief period. This would indicate that a quick wave of hair growth has again occurred in the mid-dorsal area while the lateral and ventral areas continue their growth.

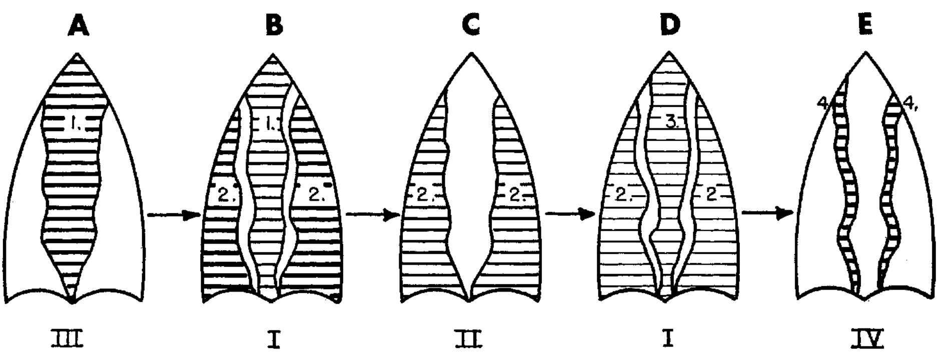
In our shearing experiments, guard hair growths sometimes occurred at least 10 days out of phase with a preceding fur hair growth. Therefore a possible explanation for this repetition of growth in the mid-dorsal area is that in the I phase preceding the II, an intensive growth of fur hair was taking place in the mid-dorsal region. After completing its growth the pattern became a II, but changed to a I again when guard hair growth darkened the mid-dorsal area. This dark center stripe faded, along with ventral and lateral pigmentation, as hair growth was finally completed and the pattern became a IV. The IV pattern shows that hair growth ceased in all areas except the dorsolateral stripe, which was now actively growing.

It may be that because there are so few guard hairs in relation to fur hairs in a pelage, only guard hair growth occurs mid-dorsally and the center stripe does not become dark. If guard hair growth began during a II pattern, the pattern would continue to be a II for some time after the initial guard hair growth. Until the growth reached a maximum there would be insufficient color on the flesh side to produce a pattern change. It would briefly become a I at the height of the growth and then turn lighter again as the growth tapered off. If the next pattern was a IV, it might be interpolated in a pattern check as being a IV well before all guard hair growth in the center stripe had ceased. This would mean that certain patterns produced by guard hair growths alone may be more apparent than real. It would also explain the quick alternation of patterns from 111 to 135 days (Fig. 15).

In older ages, the II and III patterns occurred much less frequently and I patterns appeared to change directly to IVs and vice-versa. This apparent deficiency in the number of II and III patterns may be due to a shift in the phase differential between the mid-dorsal area and the ventral and lateral areas. In shearing experiments, as the animals became older, growths in any particular area tended to be slower. This allowed adjacent areas time to begin growth before the first area was completed, and could also explain why II and III patterns might tend to merge with Is and IVs to some degree.

Direct correlations between shearing results and the pattern changes in Figure 15 are difficult to make. A new growth observed in a sheared area

Figure 16. Manner and direction of pattern change in certain age groups. All areas with the same number are the same growth of hair.



is not the beginning of growth because hair production had to begin at some prior time so that hair could grow sufficiently to be visible above the surrounding sheared hair. How long it takes from the time dark pigmentation is first visible on the flesh side of a pelt until new hair becomes visible is unknown.

Pigment patterns may make significant changes during the interval between these two periods. Because of this growth differential and the fact that the sheared kits may have been slower in development than normal wild kits, it is difficult to accurately relate the shearing diagrams to age periods for patterns.

Interpolations further complicated by the overlap between growth waves which increases with age and often makes it difficult to determine where one growth wave ends and the next begins. Perhaps the easiest way to correlate external and internal changes is by direct comparison of the expected series of sheared-kit diagrams. Through interpolation, the shearing diagrams may then be related to a probable pigment pattern.

Figure 17 is an attempt at such a correlation. The pelt patterns termed *Expected Patterns* are expected pattern changes derived from Figures 7 and 15. Each is labeled with the age span in which it is expected to occur. Dark growing areas are designated with the growth cover they represent. The column of diagrams labeled *Visible Hair Growths* contains the diagrams previously listed for sheared muskrat kit B-519 in Figure 11. Dotted lines indicate incomplete or spotty growths for a region, while concentric lines show new growth occurring before the previous growth cover has finished. The numerals in the center of each diagram give the age in days when this growth pattern appeared, and the small letters serve to designate a particular growth. All growths with like letters are the same. Small letters represent areas of growth and not complete growth covers. Thus, there are two general growth areas shown: 1) *ventral and lateral* – designated by letters (b) and (d); 2) *dorsal and dorsolateral* – designated by letters (a), (c) and (e).

The final series of diagrams termed *Probable Flesh Patterns* represent the estimated flesh patterns for muskrat kit B-519. These correlate the *Visible Hair Growth* column with the *Expected Patterns.* Alphabetical designations in the latter diagrams represent growth areas on the flesh side which are directly comparable to those in the *Visible Hair Growth* diagrams. In other words, any particular letter in either column represents the same growth. Figure 17 shows the following pelage development sequences for kit B-519:

100 *through* 111 *days of age.* The first expected pattern is a III. At 102 days, a growth of hair covers the ventral and lateral portions of the body. However, this hair has completed its growth and a mid-dorsal growth is beginning to show in spots. Considering that flesh patterns are well in advance of hair growth, this would give B-519 the expected III pattern. This new mid-dorsal growth is designated by the letter (a) on Figure 17.

111 *through* 121 *days of age.* The expected pattern is a I. At 118 days the dorsal growth (a) has completely filled in, but growth is not yet com-

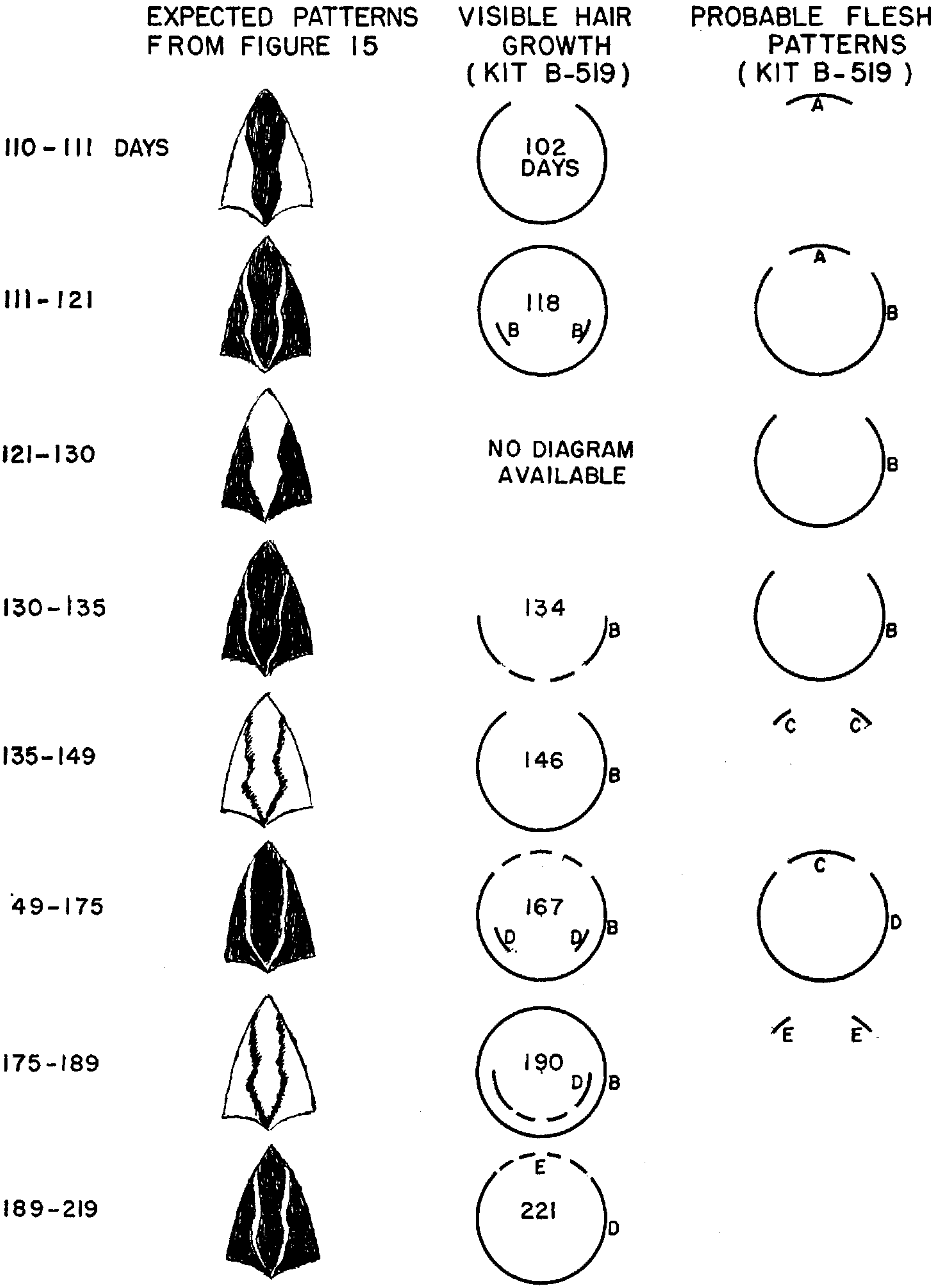


Figure 17. Correlation of expected patterns and sheared-kit diagrams

pleted. Laterally, a new growth (b) is making its appearance. Since flesh pigmentation must be well in advance of new growth, the probable flesh color is completely dark ventrally (or will be sometime within the 111 to 121-day span). Dorsally, the flesh color should also be dark, because growth (a) has not yet completed its length. Therefore, the flesh pattern at this age must be a I – again correlating with the expected pattern.

121 *through* 130 *days of age.* The expected pattern is a III, but no observations were made on B-519 during this time; consequently no diagram of hair growth is available. However, to produce a III pattern, the (b) growth (the last growth to begin) would continue to grow during this period, thus continuing the dark belly and lateral surfaces, but the (a) growth, after growing through two successive patterns, would finish its growth and the mid-dorsal area would turn white.

130 *through* 135 *days of age.* A pattern change of short duration is expected, with a darkening of the mid-dorsal area to form a I pattern once more. However, we are unable to correlate the existing growths with the expected. The (b) growth continued laterally and ventrally, but no growth could be detected or even anticipated dorsally. The animal was 134 days old when this diagram was made and at the end of its pattern range. The pattern that followed was a IV, so no I pattern was possible if the pattern to follow was to be produced within the expected range of time. The only explanation for this discrepancy is that either this is merely another case of individual variation, or else there is some variability to be expected at this point because of the short span of time involved and the fact that II patterns are also found in appreciable numbers during this period (Fig. 7) indicating that part of the patterns are forming IIs instead of Is.

135 *through* 149 *days of age.* The expected pattern is a IV and the (b) growth from previous patterns has now been completed. A new (c) growth begins along the dorsolateral line. As the sharply defined dorsolateral patterns in any pelt collection indicate, dorsolateral stripes must be produced by a narrow band of growth beginning well in advance of any growth adjacent to it. However, as this growth progresses it later spreads and fills in the area between the stripes, producing a broad mid-dorsal stripe. The expected pattern between 149 and 175 days of age is a I, which indicates that the dorsolateral stripes (c) of the previous IV pattern have begun to fill in as described above. A new (d) growth of hair has begun to show laterally and the flesh pigmentation in this area has progressed considerably beyond it to produce the I pattern expected at this age.

What constitutes any particular pattern is extremely variable. Delays and varying degrees of pigmentation make the classification of a pattern in many cases a matter of interpolation. As the animal becomes older, delayed areas and overlap in growths become more and more common, thus distorting the patterns even further.

175 *through* 189 *days of age.* An example of the effect of delays on pattern development may be seen at 190 days of age. The (d) growth, which began at 167 days, spread slowly and

irregularly across the belly to the dorsolateral line where it stopped, leaving without cover an irregularly shaped delayed area between the hind legs and several smaller ones in the chest region. The areas covered completed their growth by 190 days of age without the delayed areas showing any sign of new hair growth. The dorsolateral line may have been producing some hair, but the IV pattern was produced without ventral and lateral growth ever having begun in the delayed area.

189 *through* 219 *days of age.* The expected pattern is once more a I. The delayed areas have now been completed in the (d) growth cover and a new (e) growth has occurred middorsally. Indications are that most of the (e) growth, although broken, is nearly completed so far as hair length is concerned, thus putting the flesh-side patterns beyond the I stage. Although B-519 is 221 days of age at this stage, and is at the end of the age range for the expected I pattern, it is still comparable with the expected pattern. The ventral growths that make up the pattern are merely the filling in of delayed areas (d) that became out of phase at 190 days of age because of these delays. Dorsally, the new growth covers all except a delayed patch on the rump. Thus, delays have caused sections of a growth area to become completely out of phase with the remainder of that growth area.

Our known-age collection of pelts did not extend beyond 219 days of age, so we are unable to predict future patterns. However, the sheared animals indicate that growth does continue, but at a decreasing and irregular rate. Beyond the 5th growth cover, areas of growth become so broken and out of phase with adjacent areas that further growths are more of the adult type with an eventual complete loss of immature symmetry. The end result, of course, will be an almost complete cessation of all growth and a white pelt in the spring months. Most irregular and out-of-phase growths will occur during January and later. Sixth and 7th growth covers have been recorded in some animals, but these are incomplete and irregular.

Changes are not all simple in-line changes and complete in a single wave of pigmentation change. In some instances, the same pigmentation in an area may extend through several pattern changes. A further complication is that growth covers are not necessarily completed at a resting pattern, but may reach completion during part of a growing pattern. All these things tend to make an understanding of the primeness process difficult.

Types of Hair Growth

Our data indicate that there are two major types of hair growth taking place in muskrats, which we term developmental and seasonal. Collins (1918) held similar views concerning molts in Peromyscus: "These moults may mark different stages in the life cycle of the individual or they may be seasonal in character" (p. 73).

Developmental hair growth occurs only in immature animals and complements the growth processes of the developing muskrat. It does not seem to be dependent to any extent on the time of the year or weather, but rather on the age and physical condition of the animal. This agrees with findings concerning pelage changes in *Microtus* by Goin (1943), who stated that the time of molt is probably largely determined by the age and physical condition of the animal.

Accordingly, a 90-day-old muskrat in August will have a pelage of approximately the same quality and the same stage of development as a 90-day-old muskrat in December. Immature muskrats are continuously producing pattern changes throughout their developmental period. Developmental hair growth can be subdivided into four general pelages based mainly on hair growth covers: Nestling, juvenile, post-juvenile, and subadult. These pelages can be correlated with the first four growth covers. The *nestling* pelage is formed by the first growth cover, the *juvenile* pelage is formed by the 2nd growth cover, *post-juvenile* pelage results from the 3rd growth cover and *subadult* pelage is brought in by the 4th growth cover. Succeeding growth covers are more irregular and adult-like in their formation and are considered intermediate between subadult and adult pelages.

Nestling. At birth, hair growth in the muskrat kit is already beginning, as evidenced by the slate-blue pigmentation of the dorsal skin surface. Hamilton (1938) observed similar early hair development in the northern pine mouse. Although the time span is different, regions experiencing hair growth in early development and their sequence of change, is similar in both the pine mouse and the muskrat.

Hair growth ends at approximately 28 days of age in all areas and the flesh surfaces now become clear white. This completes the growth of the nestling pelage and all follicular activity ceases for approximately 10 days.

During the development of nestling pelage, no patterns bearing a dorsolateral stripe were found. In order, the only patterns involved are III, 0, II and V. I patterns are completely absent during this early period and only the entirely dark 0 phase can be found IV patterns are also conspicuously absent. The first complete pelage is grayish in color and has a fuzzy appearance. After a short period of quiescence (about 10 days) following the completion of the nestling pelage at 28 days of age, hair growth commences once more.

Juvenile. Our summer pelt collection which fits the juvenile pelage classification and the sheared animals in this age group fail to indicate any evidence of the occurrence of other than O, II, III, and V patterns. Dorsolateral stripes have not yet made their appearance, and only O and V phases are to be found instead of I and IV. The beginning pattern is II, and the changes probably progress through O to III and back to V (resting) once more. One of the pelts in the summer collection was an estimated 55 to 65 days of age and was found to be changing from a III to a V phase, thus indicating a likelihood that the final change to the juvenile pelage occurs in this maner. The shearing experiments give evidence that such a change does take place at this age.

The juvenile pelage, unlike the nestling pelage which starts mid-dorsally, begins laterally just posterior to the forelegs. From there it spreads caudoventrally and laterally to the mid-

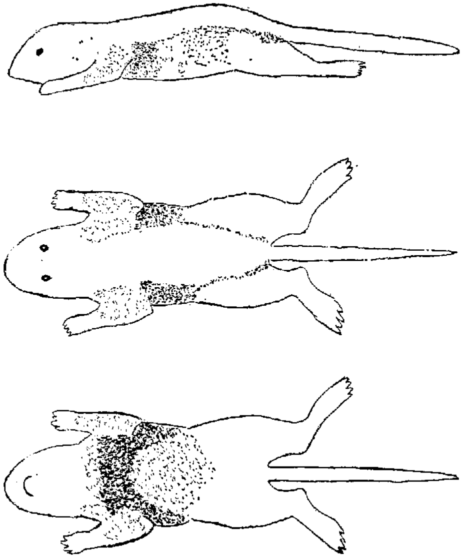


Figure 18. Lateral (top), dorsal (center), and ventral (bottom) views of a 39-day-old muskrat kit. Shading shows where growth of the juvenile pelage (2nd growth cover) is taking place.

dorsal stripe. In the chest region it also moves anteriorly to complete the coverage. As growth spreads, the mid-dorsal nongrowing stripe is delineated by the abrupt halt of the lateral growths at the dorsolateral line. It is probable that the juvenile changes cover another 30-day period of growth between 38 and 68 days of age.

In a comparison of this description with the results of the shearing experiments, the shearing diagrams indicate the progression of external hair growths and do not show an exact correlation with changes in the color of the flesh side. Flesh patterns must be interpreted from external hair growth. Thus there may be a lag between complete hair coverage externally and the cessation of growth and pigment production in the follicles. There will also be a lag between the beginning of new hair growth and the time that it first becomes visible against the old sheared pelage.

Growth of the juvenile pelage and the stage of its development may also be influenced by factors other than age. Butcher (1939) found in the white rat that quantity of the food after weaning had an effect on hair growth. It is quite possible that muskrat kits, which are weaned at approximately 30 days of age, may also reflect the effects of insufficient food in the time at which the post-juvenile growth of hair occurs and is completed. It would be wise, therefore, not to set too close a tolerance on the age at which the juvenile pelage completes its covering. A reasonable span would be from 55 to 75 days of age.

Aside from an increase in size of the animal and an increase in density of the fur, no really noticeable change in the appearance of the kit relative to color has occurred. No real shedding seems to occur and much of the existing fur is probably retained, although some replacement undoubtedly does take place. Changes in the texture or color of fur are not apparent. The muskrat still has a somewhat fuzzy appearance. However, the new hair is probably slightly longer than the growth preceding it.

Post-Juvenile. The post-juvenile pelage patterns exhibit the first sign of patterns marked with a dorsolateral stripe. The exact manner and point in pelage growth where this change to dorsolateral stripes occurs is uncertain. We have only a relatively few known-age pelts in this age group, but among them are several pelts with a dorsolateral stripe.

Pelage begins laterally behind the forelegs, as in the previous growth, and spreads up to the dorsolateral line, but when the mid-dorsal stripe fills in there seems to be a difference in the manner of growth. Instead of a diffuse growth covering the mid-dorsal area evenly, an intensive growth is well under way along the edge of the mid-dorsal area before the center begins to show signs of growth. This produces a border of longer hairs, or a dorsolateral stripe. Completion of this pelage is not followed by a period of complete follicular rest. The new subadult pelage begins immediately thereafter with some overlap of the previous growth cover. Growth cover is probably completed between 110 and 125 days of age, and hair growth somewhat later.

Post-juvenile changes bring about a gradual yet noticeable change in the character of the fur. It becomes darker in color, assuming deeper brown hues and the general sheen of the pelt is greatly increased. A considerable increase in the number of guard hairs seems to occur along with a noticeable shedding of some of the existing ones. Over-all length and density of the coat increases. In general, the texture and quality of the fur becomes more like that of the adult. The dorsal guard hairs probably increase in number and length to give the pelt a new sheen.

The significance of the dorsolateral stripe is not known. Why should the spread of ventral hair growth suddenly stop short of joining a still actively growing mid-dorsal stripe by the narrow margin of a dorsolateral stripe? What determines the initial extent of this line and what is its purpose? Is this a genetic control which comes into prominence with age, or is it controlled by the endocrine system coincident with development of sexual maturity? These questions must yet be answered.

Subadult. Somewhere near 110 days of age the 4th growth cover of subadult pelage begins (Fig. 11). It is similar in appearance to the post- juvenile, except that the density of the fur has increased. This pelage is characterized by a confusingly fast fluctuation of patterns. It seems to be a transitory period from past dominance of II and III patterns to a dominance of I and IV patterns.

Growths of hair in one pattern may be prolonged and carry over to form parts of two or even three successive patterns. This partially explains the quick pattern fluctuation during the early part of the subadult pelage development. It also explains why the IV pattern between 135 and 149 days does not mark the end of the 4th growth cover. The IV pattern between 175 and 189 days of age (Fig. 15) actually terminates it instead, because the beginning pattern for this pelage carried in it a mid-dorsal stripe which was a remnant from the post-juvenile pelage or 3rd growth cover. This was not replaced until the 175- to 189-day range after the 5th growth cover was well along (Fig. 11).

The remaining growth covers can also be considered as subadult in character, but are transitory between the true subadult pelage and the adult type of growth. The 5th growth cover is the only one completed in sheared animals, while the 6th and 7th growths begin in a fragmentary manner but only in certain individuals. These growths probably bring a further increase in density, and a gradual shift to the brighter, orange-colored fur of late winter and spring muskrats. Irregularity of patterns and delays in growth become increasingly prominent until in the latter stages of the 5th growth there is an almost complete shift to adult-type growths. Partial 6th and 7th growth covers among sheared animals appear typically adult in formation and overlap earlier growths to the extent that they are completely out of phase with all adjacent areas.

It seems as though some sort of seasonal control begins to take over as spring approaches, overpowering the symmetrical growth tendencies and depressing the growth rate. Our sheared muskrats may have shown an exaggerated irregularity during this period because of a nutritional deficiency, but the tendency toward pattern irregularity can be found in many immature pelts at this time of the year.

In considering a random, unaged group of late February muskrat pelts taken during the regular trapping season, the frequency of occurrence of III patterns increased to second in importance, being exceeded only by the V patterns. Because the largest proportion of any random collection of immature muskrats is the early born of the year, this would indicate that the final pattern phase is probably a III before the spring prime.

Seasonal pelage changes are restricted to adult muskrats and the transition period between immature and adult growth phases in the spring. Color of the pelt and fur density vary with the season. The flesh surfaces are characterized by an irregular blotchy growth pattern, in contrast to the symmetrical pattern of the developmental pelages. Anticipated changes in pattern are only expressed in general terms of increased or decreased pigmentation, as no definite patterns can be said to exist. Precise division of the pelages is difficult to make, as changes are extremely gradual due to the irregular character of the growth patterns. Age apparently has little or no effect on these pelages.

Spring. The last symmetrical pattern of immatures in spring is a III. As this gradually breaks up and disappears, irregular blotches of pigmentation make their appearance in various places, apparently beginning on the belly, neck and shoulder region. These new growths of hair appear on the fur side as patches of orange spring fur, which is considerably brighter than the dark brown winter fur. This is not to imply that all the winter fur is replaced by the new growth but rather it probably is a filling in as well as replacement, thus adding to the final density of the pelt. Gradually, in this irregular fashion, the entire pelt becomes filled in with the new growth. When this is completed the pelt is in a prime condition and hair growth has ceased with the disappearance of pigmentation on the flesh side. Hair density is at its peak and the pelt is of top quality. This would normally occur sometime in late February or the first part of March. February and March, therefore, are the months for the spring prime pelage to be attained. Muskrats which were adults from a previous year go into the spring pelage in exactly the same fashion, except that they enter with a blotched pattern instead of a III. The time of entry is the same.

Considering that this is purely a seasonal growth, it might be wondered if late-born litters acquire their spring pelage at the same time as the early litters of the same year. Observations on captive muskrats and steel-trapped animals during the spring lead us to believe that by the middle or end of March all muskrats, including late-born litters, are acquiring spring fur. Late-born muskrats probably cut short their subadult growth, skipping some of the late phases, and go directly into the spring pelt at this time. This would concur with Lavrov's (1944) findings that molts are skipped by late-born muskrats.

Summer. Following the completion of spring fur growth is a period of complete quiescence when no new hair is being produced. This usually continues until the middle of April, when irregular patches of pigmentation once again make their apeparance on the flesh side. These patches are not deeply pigmented and are scattered, so that the appearance of a rather light-colored pelt is retained. Most of the growth, signified by the appearance of the pigmented spots in the skin, is probably due to growth of new guard hair.

Shedding of winter fur begins and continues into the summer. Hair growth is continuing at a relatively slow rate and seems to lag behind shedding so that the pelt is continually becoming less dense, until in August it reaches its minimum density.

Most of the fur being shed is winter fur, but much of the spring fur may be retained along with the thin new growth being acquired. This statement is made on the basis of the appearance of summer pelts which show a yellowish color that, though somewhat lighter, is similar in color to the orange-tinged spring pelage. The lighter color could be due to losing the darker winter fur from the pelage. Pigmentation of the flesh side continues moderately through August.

Thinly furred pelts during the summer are to be expected. A heavy pelt during the warm season is not necessary and the energy needed to produce or maintain a heavy pelt can be better diverted to other body processes at a time when the muskrat is most active. This would be especially true of lactating females with a litter.

Winter. Commencing in September, pigmentation on the flesh side increases in intensity and the growth of new hair is vigorously renewed. The growth of the winter coat has begun.

Hair growth continues through the winter at a very slowly decreasing rate until spring. During this protracted growth period much of the summer fur is probably replaced and sufficient additional growth takes place to eventually bring the pelt up to full winter density. The color changes from the orange cast of the summer pelt to dark brown, with a pronounced sheen, as the dull, lusterless summer fur is replaced. This new luster can be attributed mainly to a very noticeable increase in dark shiny guard hairs.

The production of winter fur presents such slow and subtle changes as to make definite short-term progress difficult to determine. The characteristic irregular, blotchy pigmentation patterns show only slight changes in intensity except when comparison is made with the extremes. Irregular and interrupted patterns of hair growth are continually forming and reforming during the entire winter growth period like the patterns of a kaleidoscope.

Primeness Definition

The traditional theory of muskrat pelt primeness holds that the degree of pigmentation on the flesh side of the pelt is directly indicative of the degree of primeness of the pelt. Late summer pelts are completely dark but grow progressively lighter with the approach of winter until in March they are pure white when the pelts are completely prime.

Some of our findings are in disagreement with these concepts. We therefore are defining primeness as *that condition existing when the pelt is at its highest quality and the fur has reached its maximum length, density, and finest texture; when the hairs have matured with seemingly no further pigment being produced, and as a consequence, the flesh surface of the pelt appears devoid of hair root pigmentation.* A pelt is prime only when a combination of all these factors is present, and a pure white pelt is not in itself sufficient evidence of primeness.

Starvation or sickness may bring about a cessation of pigment production regardless of age or time of the year, with a resulting unpigmented and prime-appearing flesh surface; yet this fur usually is not at its top quality for density, length and texture. Nor, for the same reason, is the pelt of a lactating female with no evidence of growing hair to be regarded as prime because it has a clear and unpigmented flesh surface. Pelts from lactating females in our summer pelt collection showed some of the thinnest and poorest fur of any in the collection, yet the flesh surfaces were completely white.

Recommendations for Research

Other investigators have shown that sexing and aging by pelt pattern is a useful and simple technique for gathering mass data quickly and easily in muskrat population studies. Our material has proven the validity of the method for use at least in Wisconsin and has shown that it is accurate when checks are made by experienced personnel. We, therefore, recommend its routine use by managers and believe that its accuracy is unquestionable if the check is performed in the proper manner.

Future studies should be carried on to find out if an aging technique might be worked out on the basis of a combination of such factors as:

1. Age related to hair length in the early ages and until adult length is reached.
2. Age related to the length of the clear hyaline base of mature hairs.
3. Age related to the total number of hairs per follicle and the number of growing hairs per follicle.
4. Age related to follicular density.

An exact knowledge of how long mature hairs are retained in the pelage would increase our understanding of how pelages are replaced and also might be of use in any aging technique based on histology.

We see a need for studying hair growth and primeness in relation to the physiology of the animal if we are to more fully understand the problems involved and develop practical techniques. The interrelationship of hair growth to the life processes appears to be relatively complex and is a long way from being understood.

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