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Ontogenesis of pelage and the course of moulting in *Microtus brandti* (Radde, 1861)

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Abstract

Two methods are used in the investigation of the development of fur and moulting in small mammals. The most common way is to observe the pigmentation of the skin. We have used a more recent method, staining the whole animal with standard hair colours and observing changes in pelage patterns. It is thus possible to investigate ontogenetic changes in voles, and also the influences of different conditions of photoperiod and temperature on moulting. Contrary to the information in the literature, we found that newborns of *M. brandti* are pilose. During ontogenesis the following moults take place: I. Moult into the second immature pelage, II. moult into the first mature pelage, III. seasonal moultings (spring and autumn). Moults I. and II. occur, depending on the age of the animal.

Like other Arvicolidae *M. brandti* shows a sublateral course of moulting. The moult of the ventral body side is completed before the dorsal side. Deviations from this scheme, so-called "moulting variants", are possible.

Within one population of *M. brandti* the spring generation passes through five moults and the autumn generation through only four in the first year of life. Because of the shortened duration of moulting during low temperatures the first moults of the autumn generation are faster than those of spring-born animals.

These results represent a preliminary attempt to clarify conflicting observations on moulting from field investigations of small mammals, involving, in most cases, animals of different age classes and generations from one population.

Introduction

Investigations concerned with moulting are rare. At the beginning of this century, studies of mammalian pelt were undertaken mostly because of the commercial use of hunted game furs. Initial results were obtained from mammals that changed their fur colour. Later, the connection between moult and the state of pigmentation of the inner surface of skin was discovered. Continuous observations of hair changes in living animals are still rare, but they still offer the best opportunity for investigating the postnatal ontogenesis of moulting under different environmental conditions. We examined the moulting processes in the vole *Microtus brandti*, because of their ease in keeping, their highly developed social behaviour and our rather good knowledge of this species. The aim of the present study was to establish a general model of the moulting processes in small rodents, especially Arvicolidae.

Material and methods

Species and maintenance conditions (MC)

The vole *Microtus brandti* is a very social animal, living in large colonies and often exhibiting cyclic fluctuations and gradiations in its abundance. The species occurs throughout the steppes of Central Asia and has extended its distributional area eastwards in recent years. The vole shows a high reproductive potential and, as a diurnally active herbivore, is regarded as the most important competitor of pasture animals.

In our laboratory, voles were bred in a HAN-rotation system for rigorous outbreeding (Rapp 1982) and were kept under standard environmental conditions (21 ± 2 °C, 50–60 % humidity, L:D =

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14:10, L_{on} 4.00 a.m., light intensity ≈ 300–400 Lux). After weaning at an age of 21 days, the animals were kept in sibling groups. For these investigations voles were maintained under different conditions (MC):

MC 1: 21 ± 2 °C, L:D = 14:10 (L:D, T = const.)
MC 2: 20 ± 2 °C, L:D adapted to the natural photoperiod (L:D ~, T = const.)
MC 3: T and L:D adapted to the natural changing conditions (L:D, T ~)
MC 4: 20 ± 2 °C, LL (light throughout the day).

Feeding was the same for all animals: standard pellets and water ad lib., plus fresh food (apples, carrots, cabbage, *Taraxacum*) three times each week.

Staining and pelt investigations

To investigate moulting we used a treatment modified from Militzer (1989). Animals were anesthetized by using a 1.43 % solution of sodiumhexobarbital and then stained with standard hair colouring (Londancolor, black). Following completition of one moult, the voles were re-stained. Changes in pelage patterns were recorded weekly. For each MC, twenty animals were investigated over a timeperiod of one year. We distinguished between a spring generation (animals born in spring) and an autumn generation (animals born in late summer or autumn). To complete these studies, we observed the skin pigmentation of dead animals from the laboratory, and also from those caught between 1988 and 1990 in their natural environment near Ulan-Bator (Mongolia).

Results

Genesis of neonatal pelage

The following results are based on observations of 22 animals born in three litters. Voles are born with eyes and ears closed, and only the vibrissae are visible without the microscope; they seem to be naked. Contrary to the opinion in the relevant literature, the whole body excluding the soles is covered with short, fine hairs after birth (Fig. 1, 10 min. after birth, umbilical cord not bitten through at this time).

Table 1 gives an overview of the genesis of neonatal pelage.

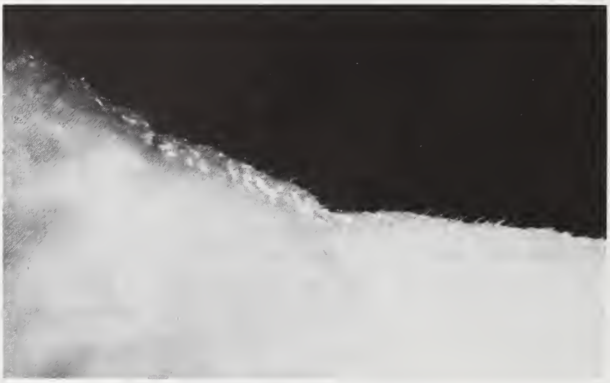

Fig. 1. Skin surface of a newborn *Microtus brandti*, 10 min. post partum

Postnatal ontogeny of fur development and moulting

After the first juvenile pelage, voles moult into a second juvenile coat and then into the mature pelage, which may be a summer or a winter fur, depending on date of birth and season. Spring-born animals pass through five moults, because the first mature coat is a summer fur. They change into a winter pelage in autumn, whereas the autumn generation

Table 1. Genesis of hair coat

Day of life	Appearance
2.	whole animal covered with downy hair, especially dorsal side and on the back of the head
3.	DS down to the top of the feet darker, VS more light coloured, vibrissae growing
5.	forefeet pilose
6.	hairs begin to grow in length (2 mm)
7.	hind feet pilose, body hairs 3 mm long
8.	vibrissae 10 mm, hairs on DS 4 mm, with some dark pile hairs in between, VS hairs 3 mm long
9.	portion of pile hairs growing, eyes start to open (up to 11th day of life)
10.	vibrissae 13 mm, DS with underwool
12.	eyes and ears open, VS with good visible underwool, DS with longer pile hairs
15.	VS hairs 5 mm long, vibrissae 15 mm long, pile hairs rising above the coat
12.–15.	development of first juvenile pelage (development of new hairs) is complete, after 15th day no skin pigmentation was found, hairs only growing in length up to 23rd day
17.	vibrissae 20 mm
20.	vibrissae 30 mm
23.	DS and VS hair length 5 mm, woolly hairs and guard hairs are fully grown, so pile hairs are no longer above the rest of the coat

VS = ventral side, DS = dorsal side of animal.

Table 2. Frequencies of moulting variants

Variants	Number (n)	Frequency (%)
Dorsal A	204	51.64
Dorsal B	17	4.31
Dorsal C	71	17.97
$\text{Dorsal}_{\text{diff}}$	103	26.08
total	395	100.00
Ventral A	53	13.45
Ventral B	216	54.82
$\text{Ventral}_{\text{diff}}$	125	31.73
total	394	100.00

moults into a winter coat with the first adult fur in the first year of life. All animals living under changing environmental conditions, and born in spring develop a second winter fur. Thus, the autumn generation undergoes only four moults in the first year.

For better understanding we defined the different courses of moulting as "variants". Excluding the moultings of senescence, *Microtus brandti* generally shows a synchronous growing of hairs. To allow systematic observation of moulting we have regarded the dorsal and ventral body surfaces as independent, although they are both one entity in moulting. The moult generally begins ventrally and advances over the flanks to the back; therefore it is completed ventrally earlier than dorsally. This course is defined as sublateral moulting by KRYLTZOV (1964). Figure 2 shows the variants of ventral moulting (A – beginning laterally and forming a band, B – beginning cranially and at the axillae; both ending at the feet and tail). Figure 3 explains the dorsal variants; all three start at the shoulders and

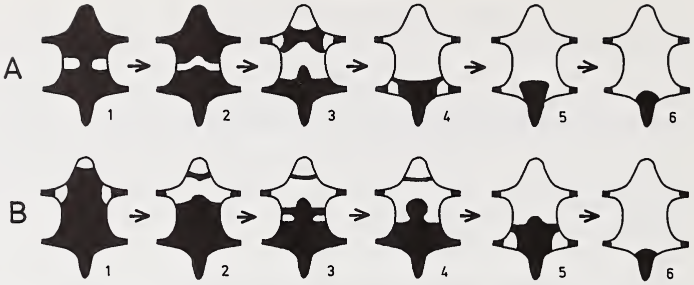

Fig. 2. Moulting variants of the ventral side, black: old coat, white: new pelage

haunches and end at the tail. Dorsally as well as ventrally the paws moult least or are excluded from the moult. The tail may also show irregularities, such that we found a "raccoon-like" marking, although the tail is always completely moulted. These described moulting variants were observed in all ontogenetic hair changes (excluding senescence) and, under each maintenance condition. They seem to be independent of abiotic factors or birth date, suggesting they may be endogenous. Table 2 shows the recorded dorsal and ventral body side variants of moulting and their frequencies. The variants $\text{Dorsal}_{\text{diff}}$ and $\text{Ventral}_{\text{diff}}$ comprise patterns, which cannot be categorized within the described variants above, and include the scattered moultings of senescence. Table 3 explains the frequencies of the observed variant combinations. Through its life time one animal can change from one moult variant combination to another. We observed that, in most cases, the first moults show other combinations than the later ones. The following changes occurred:

Table 3. **Combinations of variants and their frequencies**

Variants Dorsal/ventral	Number (n)	Frequency (%)
A/A	28	11.72
A/B	134	56.07
B/A	2	0.83
B/B	10	4.19
C/A	11	4.60
C/B	54	22.59

AA ⟶ AB, BB, CA, CB
AB ⟶ AA, BB, CA, CB
BB ⟶ AA, AB
CA ⟶ CB
CB ⟶ AA, AB, CA

Moultings of senescence (scattered moultings)

With increasing age ordered moulting begins to change to scattered patterns. Animals of higher age no longer show regular moults (Fig. 4). Normally, such a scattered moulting pattern was recorded after the first year of life, but it can also occur earlier; thus the first irregular moults can be observed in animals which are six or seven months old. These diffuse hair changes are included in the seasonal moults and are not separate entities.

Influence of age on the moulting process

Under defined maintenance conditions (MC) the start and the end of the moults from first to second juvenile pelage and from the second to the mature coat occur very close together for all animals. These dates seem to be more strongly correlated with age than the subsequent (seasonal) moultings. Figure 5 shows the duration of the spring (S) and autumn

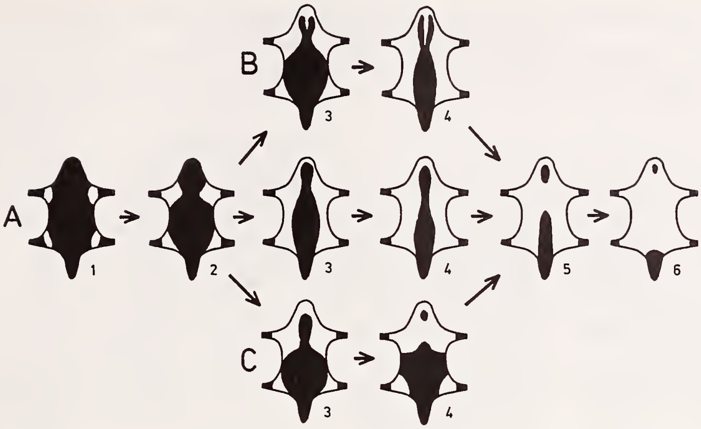

Fig. 3. Moulting variants of the dorsal side, black: old coat, white: new pelage

Fig. 4. Examples of scattered moulting; above dorsal side, below ventral side

(A) moults of animals under different maintenance conditions (MC 1, 2, 3). The first hair changes begin between the 28th and 37th day, and end between the 37th and 71th day of life. The average duration is twenty days (average between 31th to 50th day of life, dark bars within the white and structured in figure 5). Comparing the average durations of juvenile moults within the spring or autumn generation, they are nearly equal under all maintenance conditions. The spring generation simply takes longer to moult into the second juvenile coat than the autumn-born animals. Moulting into the mature fur requires the longest period (35 days for the autumn generation, 50 days for the spring generation). It starts between the 51st and 111th day of life, and finishes between the 139th and 215th day (average: start 81st to 120th, end 122nd to 158th day). Again, the autumn generation moults more rapidly than spring-born animals. The animals in MC 3 (LD, T ~) are the first to start and finish the hair changes influenced by temperature and photoperiod, whereas the animals of MC 1 (L:D, T = const.), without any "zeitgeber", show the latest dates and the largest variation in moulting times. Therefore, the moult from first into second juvenile fur seems to be very closely connected with a defined age, whereas moulting into the mature coat is influenced by day length and temperature as are, to a greater extent, the subsequent seasonal moults.

Table 4 shows the results of various authors for the commencement and the end of the first and second moults during postnatal ontogenesis in Arvicolidae and Muridae (after BÜHLOW 1970, completed).

Table 4. **Commencement and end of moulting into the second juvenile and into the first adult coats of some Arvicolidae and Muridae**

Authors		Species	First into second juvenile coat Age (days) Start	End	Second juvenile into first mature coat Age (days) Start	End
Becker	(1952)	*Rattus norvegicus*	42	84	75	–
Borum	(1954)	*Mus musculus*	30	46	60	–
Collins	(1923)	*Peromyscus maniculatus*	28	56	60	–
Dry	(1926)	*Mus musculus*	18	35	45	–
Ecke and Kinney	(1956)	*Microtus californicus*	25	45	60	–
Frank and Zimmermann	(1956)	*Microtus oeconomus*	–	56	–	–
Fullagar	(1967)	*Apodemus sylvaticus*	35	50	56	–
Fullagar	(1967)	*Apodemus flavicollis*	–	–	63	–
Kästle	(1953)	*Micromys minutus*	28	44	–	–
Kemper	(1976)	*Pseudomys novaehollandiae*	–	–	35	105
Langenstein-Issel	(1950)	*Pitymys subterraneus*	–	50	–	–
Linzey and Linzey	(1967)	*Ochrotomys nuttalli*	31	87	–	–
Mazak	(1962)	*Clethrionomys glareolus*	30	75	–	–
McManus and Zurich	(1972)	*Meriones unguiculatus*	32	55	58	112
Militzer	(1987)	*Mesocricetus auratus*	–	111	112	155
Stein	(1960)	*Microtus arvalis*	23	54	59	–
Sykora	(1959)	*Microtus arvalis*	20	–	–	–
Viitala	(1981)	*Clethrionomys rufocanus*	26	60	59	88
Stubbe and Wiegand	(this study)	*Microtus brandti*	31	50	81–120	122–158

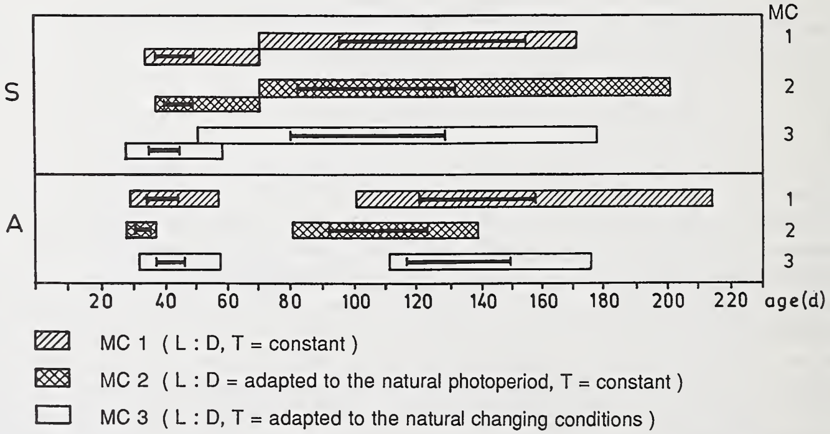

Fig. 5. Start and end of age-dependent juvenile moults; S: spring generation, A: autumn generation

Comparative studies on pelts

In addition to the observations on living animals, we have also investigated pelts of dead animals (N = 1158, MC 1 – n_1 = 728, MC 2 – n_2 = 330, pelts of animals caught in Mongolia – n_3 = 100).

The results of both methods agree completely, but with stained living animals it is possible to follow all moults through the life of one animal and, in the end, we required about 7000 voles less for the present study by staining the animals as we had used only the old method to observe skin pigmentation. Figure 6, for example, shows some typical patterns of juvenile moulting of killed animals. Hair replacements are visible in the epidermis by the pigment production of melanocytes, which were accumulated before the hair follicles maturate (RYDER 1973). The colour of the pigmentation is therefore extremely dark in the areas of active hair growth and becomes lighter as the hairs change and growth ceases (VIRO and KOSKELA 1978). Figure 6 shows the beginning (left), middle and end phases (right) of the second juvenile moult. The left picture conforms with variant A2, the middle with A3 and the right with A5 from figure 3.

Fig. 6. Typical skin patterns of juvenile moultings; left: start, right: endphase of moult

Discussion

According to many mammalogists, neonates of small rodents are born with a nude body surface except for the vibrissae, 1 to 2 mm in length (TOLDT 1935; NIETHAMMER and KRAPP 1978, 1982). BAKE (1981), SYKORA (1959) and STEIN (1960) reported on *Microtus arvalis* that the first hair tips appear on the second day of life. For *Pitymys subterraneus* LANGENSTEIN-ISSEL (1950) stated that, on the day of birth, 0.5 mm long, light hair tips can be seen under a magnifier. SCHRÖPFER (1977) found the first hair fuzz on the dorsal side on the third day of life and sinus hairs one day earlier. FRANK and ZIMMERMANN (1956) observed the first dark hairs in *Microtus oeconomus* on the second day of life. COLLINS (1923) also determined this date for the genus *Peromyscus*. In *Microtus agrestis* the hair colouration is visible on the fourth day of life (NIETHAMMER and KRAPP 1982). For *Micromys minutus* opinions vary: SLEPSOV (1947) observed the first hairs on the fourth day and KÄSTLE (1953) on the second day of life.

We have studied newborn *Microtus brandti* 10 minutes after birth, and by use of a binocular microscope observed sparse, small hairs over the entire body surface, as well as vibrissae. This differs from the general opinion; only KOURIST (1957) also described colourless hairs over the entire body a few hours after birth in *Cricetus cricetus*. It is our opinion that the type of hair development noted in *Microtus brandti* is also common in other Arvicolidae; we also found it in *Alticola semicanus,* the high mountain vole.

The genesis of neonatal pelage seems to be comparatively uniform; we only observed individual variations of 1 or 2 days. The representation given may be a general guide to the genesis of first juvenile pelage, not solely in *Microtus brandti*. The following authors gave the same developmental states: LANGENSTEIN-ISSEL (1950) delimited the end of development of the neonatal coat of *Pitymys subterraneus* between 12 and 14 days; BAKE (1981), FRANK and ZIMMERMANN (1956), STEIN (1960) and SYKORA (1959) cited the 14th day for *Microtus arvalis* and KÄSTLE (1953) the 15th for *Micromys minutus*.

Hairs have a limited life span. After the duration of the growth process, they die and are rubbed off during moulting. TOLDT (1935) distinguished between the periodic or seasonal moults which occur in wild mammals of cold and temperate zones, and the continuous (partial) moults of domesticated animals and humans. According to TOLDT (1935) animals of tropical and arctic zones, or adapted to aquatic habitats, show only one moult per year. A companion paper to this publication (STUBBE and WIEGAND 1994) will deal with seasonal moults in *Microtus brandti*.

Concerning the course of moulting, synchronous and asynchronous hair growth has been described. In *Microtus brandti* we found synchronized hair growth. KRYLTZOV (1964) noted sublateral moulting, with only minimal variations, in 18 species of Arvicolidae, LANGENSTEIN-ISSEL (1950) for *Pitymys subterraneus*, and ECKE and KINNEY (1956) for *Microtus californicus*. In evolutionary terms all these are comparatively "young" species. Primitive genera change their hair coat according to other patterns; *Clethrionomys*, in particular, shows the so-called cephalo-sacrale type. In *Microtus brandti* the sublateral type of moulting was corroborated and described from the investigation of stained living animals.

The scattered moulting of senescence has been observed by various authors: BAKE (1981) described this for 9- to 15-month-old *Microtus arvalis,* COLLINS (1918) – *Peromyscus* spec.; BECKER (1952) – *Rattus norvegicus*, ESPAÑA et al. (1985) – *Mus spretus;* BÜHLOW (1970) – *Arvicola terrestris;* and KRYLTZOV (1964) for some *Microtus* species. OLIVEIRA et al. (1992) found different pelages in sexually active males and females of *Marmosa incana*, but did not note any influence of seasons. ROWSEMITT et al. (1975) found a relationship between diffuse moulting and reproductive activities, but we have the impression that gravidity simply accelerates normally occuring moults. Generally, ageing processes were considered a primary premise of irregular moults. This is also our opinion, derived from observations on animals kept under MC 4 (T = const., LL), which age more rapidly than other voles because of light stress, and already show scattered moulting patterns within 5 months.

There is general agreement with regard to the induction of juvenile moults. Our observations show that the changes from first to second juvenile, and from there to the first mature coat, are not dependent on season, but we did find a close correlation between age and the start of these moults.

From a comparison of *Microtus* species a high correspondence of dates is evident, and the results from *Microtus brandti* also coincide closely. This high conformity, and the small possibility of the influence of exogenous factors, indicate the probability of an age-dependent course in juvenile moults. These results agree with those of LANGENSTEIN-ISSEL (1950), STEIN (1960) and VIITALA (1981). VIITALA (1981) refered to the influence of exogenous factors (temperature) on the duration of moults, and from keeping animals under different temperature regimes in the laboratory. Animals under colder conditions changed their hair coat faster than animals in warmer environments.

In our study, we found moult duration to be dependent on birth date (spring or autumn) and on abiotic factors (day length and temperature). The influence of abiotic factors on juvenile moults, however, is not as strong as in the subsequent adult moults. The seasonal dependence of mature hair changes will be discussed in the companion paper (Stubbe and Wiegand 1994).

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Zusammenfassung

Ontogenese des Haarkleides und Fellwechselverlauf von Microtus brandti (Radde, 1861)

Neben dem üblichen Verfahren, den Fellwechsel bei Kleinsäugern anhand der Pigmentierung der Hautunterseite abgebalgter Felle zu beurteilen, wurde mit Hilfe der Methode des Einfärbens der Tiere mit einem herkömmlichen Haarfärbemittel und der wöchentlichen Aufzeichnung der entstehenden Fellmuster eine Beobachtung des Mausergeschehens am lebenden Tier möglich. Somit konnte nicht nur der Mauserverlauf während der Ontogenese, sondern auch der Fellwechsel bei Einfluß der Photoperiodik und von Temperaturänderungen an ausgewählten Tieren über längere Zeiträume beobachtet werden.

Entgegen der in der Literatur vertretenen Auffassung wurde erstmals eine Behaarung neugeborener Tiere nachgewiesen. Innerhalb der Ontogenese treten folgende Härungen auf: I. Fellwechsel in das 2. Jugendkleid, II. Fellwechsel in das 1. Alterskleid, III. saisonale Haarwechsel (Frühjahr und Herbst). I. und II. verlaufen altersabhängig.

Insgesamt zeigt *Microtus brandti* wie auch andere Arvicolidae einen sublateralen Mauserverlauf. Der Fellwechsel der Ventralseite ist eher abgeschlossen als der der Dorsalseite. Abweichungen von diesem Schema, sogenannte „Mauservarianten", sind möglich. Innerhalb einer Population durchläuft die Frühjahrsgeneration fünf, die Herbstgeneration nur vier Haarwechsel im ersten Lebensjahr.

Die vorliegende Studie möchte zur Klärung der sich häufig widersprechenden Beobachtungen des Fellwechsel bei im Freiland gefangenen Kleinsäugern beitragen, die durch den gleichzeitigen Fang von Tieren verschiedener Altersklassen und Generationen entstehen können.

References

Bake, U. (1981): Beitrag zum Aufbau des Haarkleides und zum Haarwechsel der Feldmaus *Microtus arvalis* (Pallas, 1779). Säugetierkdl. Inf. **5**, 3–49.

Becker, K. (1952): Haarwechselstudien an Wanderratten (*Rattus norvegicus* Erxl.). Biol. Zbl. **71**, 626–640.

Borum, K. (1954): Hair pattern and hair succession in the albino mouse. Acta pathol. microbiol. scand. **34**, 521.

Bühlow, E. (1970): Untersuchungen über den Haarwechsel bei Schermäusen, *Arvicola terrestris* (L., 1758). Zool. Anz. **184**, 18–32.

Collins, H. H. (1918): Studies of the moult and of artificially induced regeneration of pelage in *Peromyscus*. J. Exp. Zool. **27**, 73–99.

Collins, H. H. (1923): Studies of the pelage phases and of the nature of the color variations in mice of the genus *Peromyscus*. J. Exp. Zool. **38**, 45–107.

Dry, F. W. (1926): The coat of the mouse. J. Genet. **16**, 287–340 .

Ecke, D.; Kinney, A. (1956): Aging meadow mice, *Microtus californicus*, by observation of moult progression. J. Mammalogy **37**, 249–254.

España, M.; Palomo, M. J.; Zamorano, E. (1985): Moulting and hair covering of *Mus spretus* from southern Spain. Spixiana **8**, 1–16.

Frank, F.; Zimmermann, K. (1956): Zur Biologie der Nordischen Wühlmaus (*Microtus oeconomus stimmingi* Nehring). Z. Säugetierkunde **21**, 58–83.

Fullagar, P. J. (1967): Moult in field mice and the variation in the chest markings of *Apodemus sylvaticus* (Linné, 1758) and *Apodemus flavicollis* (Melchior, 1854). Säugetierkundl. Mitt. **15**, 138–149.

Kästle, W. (1953): Die Jugendentwicklung der Zwergmaus (*Micromys minutus soricinus* Her., 1789). Säugetierkundl. Mitt. **1**, 49–59.

Kemper, C. M. (1976): Maturational and seasonal moult in the New Holland Mouse, *Pseudomys novaehollandiae*. Aust. Zool. **19**, 9–17.

Kourist, W. (1957): Das Haarkleid des Hamsters (*Cricetus cricetus cricetus* Linné, 1758). Wiss. Z. Univ. Halle, Math.-Nat. **VI/3**, 413–438.

Kryltzov, A. I. (1964): Moult topography of Microtinae, other Rodents and Lagomorphs. Z. Säugetierkunde **29**, 1–17.

Langenstein-Issel, B. (1950): Biologische und ökologische Untersuchungen über die Kurzohrmaus (*Pitymys subterraneus* DeSelys-Longchamps). Z. Pflanzenbau und Pflanzenschutz **1**, 145–183.

Linzey, D. W.; Linzey, A. V. (1967): Maturational and seasonal molts in the Golden mouse, *Ochrotomys nutalli*. J. Mammalogy **48**, 236–241.

Mazak, V. (1962): Zur Kenntnis der postnatalen Entwicklung der Rötelmaus, *Clethrionomys glareolus* Schreber, 1780. Acta soc. zool. Bohemoslov. **26**, 77–104.

McManus, J. J.; Zurich, W. M. (1972): Growth, pelage development and maturational moults of Mongolian gerbil *(Meriones unguiculatus)*. Amer. Midl. Nat. **87**, 264–271.

Militzer, K. (1987): Die Ontogenese der Haarwachstumszyklen beim Goldhamster (*Mesocricetus auratus* W.) – makroskopische und histometrische Befunde an 2 Stämmen. Z. Versuchstierk. **29**, 181–192.

Niethammer, J.; Krapp, F. (Eds.) (1978): Handbuch der Säugetiere Europas. Vol. **1**: Rodentia I. Wiesbaden: Akad. Verlagsges.

— — (Eds.) (1982): Handbuch der Säugetiere Europas. Vol. **2/I**: Rodentia II. Wiesbaden: Akad. Verlagsges.

Oliviera, J. A. De; Lorini, M. L.; Persson, V. G. (1992): Pelage variation in *Marmosa incana* (Didelphidae, Marsupialia) with notes on taxonomy. Z. Säugetierkunde **57**, 129–136.

Rapp, K. G. (1982): HAN-Rotation – a new system for rigorous outbreeding. Z. Versuchstierk. **14**, 133–142.

Rowsemitt, C.; Kunz, T. H.; Tamarin, R. H. (1975): The timing and patterns of molt in *Microtus breweri*. Occ. Papers Mus. Nat. Hist. Univ. Kansas **34**, 1–11.

Ryder, M. (1973): Hair. Studies in Biology **41**. London: Arnold.

Schröpffer, R. (1977): Die postnatale Entwicklung der Kleinwühlmaus, *Pitymys subterraneus* De Selys-Longchamps, 1836 (Rodentia, Cricetidae). Bonn. zool. Beitr. **28**, 249–268.

Sleptsov, M. (1947): On the biology of *Micromys minutus ussuricus*. Ham. Contr. Faune et Flore de l'USSR, N.S., Sect. Zool. **8**, 69–100.

Stein, G. H. W. (1960): Zum Haarwechsel der Feldmaus (*Microtus arvalis* Pallas, 1779) und weiterer Muroidea. Acta theriol. **3**, 27–44.

Stubbe, A.; Wiegand, S. (1994): Influence of photoperiod and temperature on moulting processes in *Microtus brandti* (Radde, 1861). Z. Säugetierkunde (im Druck).

Sykora, J. (1959): Die postnatale Entwicklung der Feldmaus. Der postnatale Prozess der Wachstumsveränderungen bei 1 bis 21 Tage alten Tieren. In: Hraboš polní *Microtus arvalis*. Ed. by J. Kratochvíl, F. Balát, Č. Folk, I. Grulich, J. Havlín, V. Holišová, K. Hudec, J. Pelikán, B. Rosicky, I. Sykora, Z. Šebek und M. Zapletal. Praha: Naklad. ČSAV, Pp. 53–60, 322.

Toldt, K. (1935): Aufbau und natürliche Färbung des Haarkleides der Wildsäugetiere. Leipzig: Dtsch. Ges. Klein- und Pelztierzucht.

Viitala, J. (1981): Hair growth patterns in the vole *Clethrionomys rufocanus* (Sund.). Biol. Res. Rep. Jyväskylä 7, 3–17.

Viro, P.; Koskela, P. (1978): Moult topography, moulting and structure of the fur in the Harvest mouse. Acta theriol. **23**, 503–517.

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