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Moult Topography, Moulting and the Structure of the Fur in the Harvest Mouse

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An examination was made of the moult patterns, moulting and the structure of the fur based on 304 pelts of harvest mouse, Micromys minutus (P a 11 a s, 1778) obtained from the western part of Central Finland during the period September—January. This material included 150 individuals in the process of moulting. The moult pattern in the adult harvest mouse was predominantly of the caudad or cephalad type and rarely of the dorsad type. No differences in this pattern were to be noted in respect of sex, pelage type or season of the year. This pattern is distinct from that found in all other Muridae species studied, amongst which the dorsad type is the most common, a feature which is apparently related to the typical climbing habit of the harvest mouse. The winter fur was 9-15% longer than the summer fur and 15% more dense, properties that are generally accepted as associated with thermoregulation. The fur of the young specimens was equivalent to the winter fur in length, but was the least dense of all the types studied. Those individuals already possessing the winter fur type were frequently still at the moulting stage (41-80% in the various months), so that this may represent the 'intermediate winter fur' which appears to develop directly from the juvenile fur by a simple increase in density, principally of the woolly hairs, with no intervening summer fur. In this way the length of the juvenile coat would be of ecological significance for the young born in late summer in assisting the preparation for wintering. The majority of individuals, 73%, possessed their winter fur at least a month before the 0° C isotherm was reached, and all the specimens did so by the onset of the permanent snow cover? The results indicate that the harvest mouse has adapted well to the northern environment.

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I. INTRODUCTION

The coat of most mammals varies in structure with age and season of the year, its renewal generally following one of a number of clearly defined topographic models. In the family *Muridae* these seasonal changes and the changes from the juvenile to adult coat proceed according to the dorsal model, while a more diffuse pattern is found

in older individuals (Kryltzov, 1964; Ling, 1970). The harvest mouse, however, appears to be an exception in this respect, since the moult pattern in the young is principally of the caudad type, and the dorsal type occurs only on rare occasions (K \ddot{a} stel, 1953).

Seasonal changes in the fur having an adaptive thermoregulatory function have been described in small mammal species including *Peromyscus* (Sealander, 1951) *Apodemus* (Haitlinger, 1968; Gergilevich & Smirnov, 1970), *Sorex* (Borowski, 1958), *Microtus* (Khateeb & Johnson, 1971) and *Clethrionomys* (Mazák, 1962; Sealander, 1972), and in larger animals including *Vulpes* (Basset & Llewellyn, 1949), *Capreolus* (Johnson & Hornby, 1975) and *Cervus* (Ryder & Kay, 1973). Properties affected in this way are the colour of the fur and the length, diameter and density of the hairs.

The colour of coat of the harvest mouse is known to vary somewhat with age and the season of the year. The present work aims to complete the picture of moulting patterns in this species by concentrating upon the moult in adult harvest mice and sets out to investigate moult patterns and the structure of the fur in autumn and winter in a population in the western part of Central Finland.

II. MATERIAL AND METHODS

The material studied comprised the pelts of 304 harvest mice, 175 of which were trapped at Haapavesi in September and October 1972 and 1973 (Koskela & Viro, 1976), 58 at Ilmajoki in December and January 1961-62 (Sułkava & Sulkava, 1967) and 71 in and around Oulu in September-January 1971-72. The pelts are preserved in the Zoological Museum of the University of Oulu.

The study of the moulting patterns and the general course of moulting was based on the total material, while the detailed description of the fur structure was limited to one homogeneous population, the 43 individuals trapped at Haapavesi which represented prime (non-moulting) summer, winter or juvenile coats.

The occurrence of moulting was determined on the basis of the black pigment visible on the reverse side of the pelt. This pigment is extremely dark in colour in the area of active hair growth and becomes lighter (due to a reduction in the number of pigmented follicles) as hair change and growth cease. Isolated patches of pigmentation of less than 0.25 cm^2 in area were interpreted as bites or other wounds and ignored for the present purpose (cf. Stein, 1960). No examination was made here of the fur on the limbs or tail. The moult type, or direction of advance, determined from the differential amounts of this pigment and the colour and structure of the coat. The moult types are labelled using the terminology proposed by Ling (1970), in which the direction of advance is indicated by an adverbial suffix.

The density of the fur was determined from a sample of the pelt of area 0.605 mm^2 with fur, extracted using a circular blade from a point in the centre

of the back equidistant from the tail and ears. The area of each sample was checked under the microscope using an ocular micrometer and the density of the hairs determined and expressed per square millimetre.

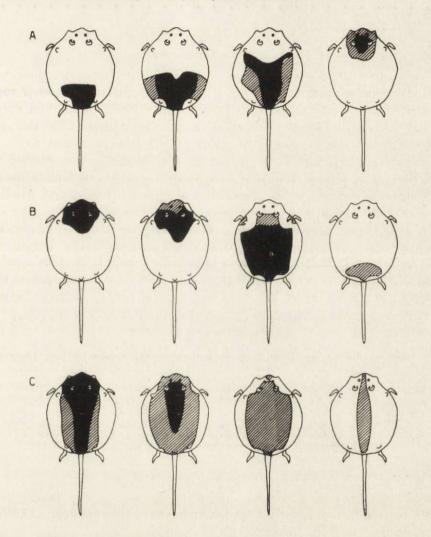


Fig. 1. Advance of moulting in the harvest mouse in the three moult types observed.

A=cephalad, B=caudad, C=dorsad. Black area=active hair follicles (anagen: Dry, 1926), shaded area=wintering follicles (catagen). The specimens described were trapped at Haapavesi in autumn and were gaining their winter coats.

The length of the coat was examined by shaving the hairs off this same sample across the surface of the skin and immersing these in a mixture of water, with a low addition of detergent; the purpose being to lower the surface tension of pure water, thus enabling the hair to float providing an easy view of each

individual hair whilst on the microscope slide. All the guard and pile hairs in each sample (2-10 in number) and 10 woolly hairs, according to the terminology of Toldt (1935), were measured for each sample, again using an ocular micrometer.

III. RESULTS

1. Moult Topography

Three types of moult could be detected in the harvest mouse pelts: caudad, cephalad and dorsad (Fig. 1). In the cephalad type coat regeneration begins in the sacral area of the lower dorsum and then spreads to the rest of the dorsum, the ribs, neck and stomach, the last areas affected being the stomach, the sides of the head and the neck. The caudad type is precisely the reverse of this, while the dorsad type features regeneration from the lower parts of the ribs and head on both sides, advancing to the stomach and upper rib area and finally to the back, the last area affected being the middle of the dorsum.

The dominant patterns observed here were the caudad and cephalad types, occuring in broadly equal proportions, while the dorsad type was rare (Table 1). No type was especially concentrated in any one season, coat type or sex, nor were any significant differences found between the frequencies of the moult types at the three locations studied.

Table 1

Occurrence of the various moult types in the harvest mouse by sex. Unknown = unidentified moult type which may be cephalad, caudad or dorsad.

	Cephalad		Caudad		Dorsad		Unknown		Total
	n	0/0	n	0/0	n	0/0	n	0/0	1014
ਹੈ ਹੈ	38	48.1	20	25.3	4	5.1	17	21.5	79
99	25	35.2	21	29.6	5	7.0	20	28.2	71
Total	63	42.0	41	27.3	9	6.0	37	24.7	150

2. General Observations on Moulting

Individuals in the process of moulting accounted for $49.3^{\circ}/_{\circ}$ of the total material, the monthly proportions varying between $29.6^{\circ}/_{\circ}$ in January and $71.4^{\circ}/_{\circ}$ in November (Figs. 2 & 3).

Grey juvenile coats were found during the period up to and including November, while the last prime summer coats were encountered in October. One individual still in the process of gaining its winter fur was found in November, and three cases were noted of animals passing directly from the juvenile to the winter fur with no intervening summer fur. Cases of winter fur were to be found from September $(73^{0}/_{0})$ onwards, and this was the only type noted in December and January. Evidence of moulting was still to be seen in the majority of the winter

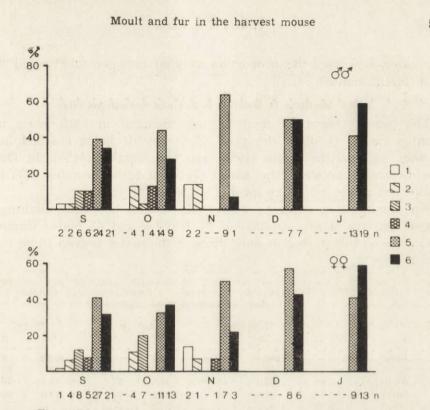
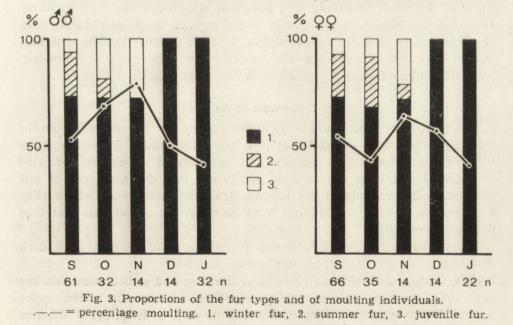


Fig. 2. Distribution of the pelts by fur type and pigmentation.
1. Prime juvenile fur, 2. pigmented juvenile fur, 3. prime summer fur, 4. pigmented summer fur, 5. prime winter fur, 6. pigmented winter fur.



fur cases, however, the proportion varying between $29.6^{\circ}/_{\circ}$ and $80.0^{\circ}/_{\circ}$ in different months.

3. Moulting in Relation to Sex and Sexual Activity

The general trend in moulting was identical in both sexes in all months except October, the peak of the moult being reached in November in both the males $(75^{\circ}/{\circ})$ and the females $(64^{\circ}/{\circ})$. In October the difference between the males $(59^{\circ}/{\circ})$ and the females $(43^{\circ}/{\circ})$ was significant at the indicative level $(\chi^2=3.55, p<0.10)$.

An attempt was made to study the relation between moulting and sexual activity in a population of 91 females and 63 males trapped at Haapavesi (Table 2), but as only three of the males proved to be mature

Table 2 Percentage occurrence of moulting in sexually inactive and active females from Haapavesi by fur types in September and October. n=number of harvest mice studied.

	Inactive		Active		Total	
	0/0	n	0/0	n	0/0	n
Juvenile fur	100.0	6	0.0	0	100.0	6
Summer fur	50.0	4	27.2	11	33.3	15
Winter fur	62.3	53	29.4	17	54.3	70
Total	65.0	63	28.6	28	53.9	91

the material was deemed inadequate in this respect. The females studied, however, presented 28 sexually active examples, almost one third of the total, including two pregnant specimens and two suckling. Moulting was highly significantly less frequent in these (28.6%) than in the sexually inactive cases (65.0%): t=3.49, p < 0.001). The distribution of coat types in the sexually active individuals was the following: juvenile, none; summer coat. 73.3%; winter coat, 24.3%.

4. Structure of the Fur

Three types of hair could be distinguished in the fur samples from the centre of the back: guard hairs, pile hairs and under or woolly hairs (Fig. 4), the characteristic lengths and densities of which are indicated in Tables 3 and 4 for the various coat types. Two distinct types of pile hair could be recognized, the longer, straighter, darker of which (Fig 4:2) may well be a transitional form between the guard hair and true pile hair types.

The guard hairs were 6.5-9 mm in length, stout, straight and dark throughout in all fur types, while the pile hairs were 5.5-7 mm in length, straight and brown in colour at the base and either wider, darker and curled over at angle or else curved with a brown tip in the upper part, and the woolly hairs slender and sinuous with a length of 5-6.5 mm

All the hair types were longer in the winter coat than in the summer one, the mean difference being 1.2 mm (t=4.96, p < 0.001) in the guard hairs, 0.6 mm (t=3.14, p < 0.005) in the pile hairs and 0.6 mm (t=5.30, p < 0.001) in the woolly hairs (Table 3). No significant sex-specific differences were noted in any of the fur types. The hair lengths for

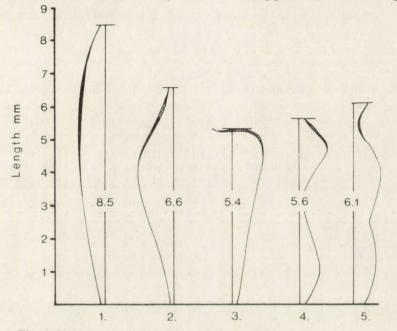


Fig. 4. Hair types: 1. guard hair, 2. long pile hair, 3. short pile hair, 4. & 5. woolly hairs.

the juvenile fur were of the same order as those for the winter fur, but in view of the small number of grey individuals a statistically significant difference with respect to the summer fur could only be established in the case of the guard hairs (t=3.19, p < 0.005).

Table 3

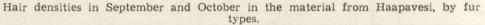
Hair lengths in September and October in the material from Haapavesi, by fur types. $\bar{x}{=}mean,$ S.E.=standard error.

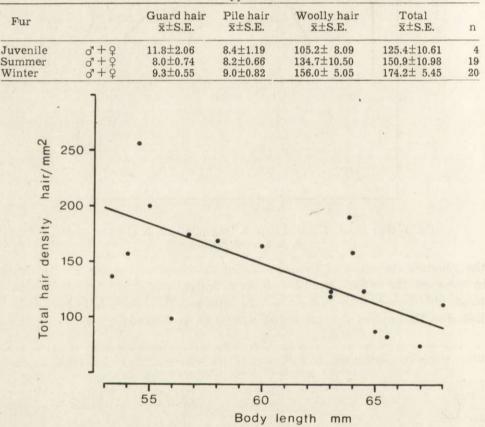
Fur		Guard hair x±S.E.	Pile hair x±S.E.	Woolly hair x±S.E.	n
Juvenile	o* + 9	8.2 ± 0.31	6.3 ± 0.31	5.6 ± 0.25	4
Summer	$\sigma' + \dot{\varphi}$	7.1 ± 0.15	5.8 ± 0.14	5.3 ± 0.08	17
Winter	d" + ♀	8.3 ± 0.19	6.4±0.13	5.9 ± 0.08	19

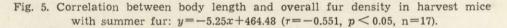
The density of the fur is determined largely by that of the woolly hairs, which are in the majority in every case, constituting $80-90^{\circ}/_{\circ}$ of all hairs. Thus the summer coat of the female was less dense than that of the male precisely because of this difference in the woolly hairs,

the latter showing a discrepancy of 35 hairs/mm² (t=1.76, p < 0.10) and an overall difference for the fur of 36 hairs/mm² (t=1.72, p < 0.20), although these differences did not reach the significant level due to the great standard deviations. The density of the guard hairs and pile hairs was practically identical in all the fur types and in both sexes. The winter fur is denser than the summer fur, the overall difference being one of 23 hairs/mm² (t=1.90, p < 0.10) and that in respect of the woolly hairs 21 hairs/mm² (t=1.83, p < 0.10) (Table 4).

Table 4.







A negative correlation was found between body length, an indicator of surface area of pelt, and density of fur in the case of the summer coats, where the greatest size differences were noted (r=0.55, p < 0.05, Fig. 5).

IV. DISCUSSION

The harvest mouse develops its »infant fur« at an age of eight days, and the moult to the juvenile fur begins at one month, lasting anything from two weeks to two months.

The moult of the juvenile coat in the harvest mouse is principally of the cephalad type, and it is only in exceptional cases that it follows the dorsad pattern, begins from the middle of the back or is nonsymmetrical, *i.e.* diffuse (Kästle, 1953). The present results, suggesting a predominance of the caudad and cephalad types with only rare occurrences of the dorsad type show a basic similarity to the pattern noted in juveniles, but depart from this pattern in two respects, the appearance of a caudad type and the lack of any diffuse type.

The moult pattern of the harvest mouse, both juvenile and adult, differs from that of other *Muridae* species studied to date, in which the dorsad type prevails throughout except in old individuals, where a diffuse moult is general (Kryltzov, 1964; Ling, 1970).

Attempts have been made to employ a moult typology in connection with phylogenetic questions in the European and Asian wild horse (M a z á k, 1962) and in rodents and lagomorphs (K r y l t z o v, 1964). Used as a phylogenetic measure, moult type would suggest that the harvest mouse is only distantly related genetically to all the other *Muridae* which have been studied from this point of view, e.g., Mus, *Rattus, Apodemus*, etc. (cf. D r y, 1926; D u r w a l d & R u d a l l, 1949; K r y l t z o v, 1964), a conclusion which would seem improbable in the light of the morphological similarities involved. In this case an alternative explanation may be sought in the form of some connection between the exceptional moult type of the harvest mouse and its typical climbing mode of existence, in support of which it may also be noted that the squirrel, *Sciurus vulgaris* L., another climbing species, also has moult patterns of the caudad or cephalad type (K r y l t z o v, 1964).

Although the ecological significance of the moult itself is well known, little has yet been said concerning the relevance of the various moult patterns. Some practical significance has been attributed to the relationship between the insulation capacities of different parts of the pelage of lagomorphs in northern and arctic areas and the seasons of the year, however, so that the dorsad mode of the autumn moult may be interpreted as enabling the thicker winter coat to develop first on the stomach of the animal, while the ventrad type of moult in spring ensures that it is this same area which loses its winter coat last (L y m a n, 1943; S e v e r a i d, 1945; H e w s o n, 1958, 1963).

It has also been suggested that certain properties of the coat deriv-

ing from differential directions of advancement of the moult may furnish an animal with special advantages when moving through the undergrowth or when seeking cover from other animals (Ling, 1970). This hypothesis is unable, however, to explain the seasonal changes in moult type noted in certain species, e.g. the mole (Godfrey & Crowcroft, 1960), or age-related changes in such creatures as the muskrat (Schofield, 1955; Linde, 1963) or the lemming (Koponen, 1964). Similarly the idea that the alternation between a cephalad and caudad moult type in the harvest mouse may be due to any greater protection afforded by the intermediate variations in colour seems questionable, since the colour changes involved on moulting are extremely small and the species in any case moves chiefly at dusk or by night (SaintGirons, 1959; Cross, 1970; Koskela & Viro, 1976).

It may, however, be conjectured in the present case that since the period of moulting is characterized by a thickening of the pelt (H y v \ddot{a} -rinen *et al.*, 1971), even to the extent of hampering movement in small mammals (B or o w s k i, 1968), a moult which begins at the head or the lower body would ensure a greater suppleness of movement than one which began in the rib area. Thus the cephalad and caudad types would be of advantage to an animal with climbing habits such as the harvest mouse.

At its first moult to an adult coat the harvest mouse may gain either winter or summer fur, a change directly to the winter fur apparently being a common occurrence in juveniles born in late summer, since the majority of the present September catch $(73^{\circ}/_{\circ})$ consisted of young immature individuals with winter fur. Three actual examples of this change in progress were also recorded.

The fur types differ in both colour and structure. The juvenile fur is tinged with grey, features long hairs, but is less dense, while the adult summer fur is reddish brown on the back and white underneath, shorter, but denser and the winter fur grey again, with only a reddish brown patch on the back, long and the densest of the three types.

The results showed the hairs comprising the winter fur to be $9-15^{0}/_{0}$ longer than those of the summer fur, with corresponding differences of $15^{0}/_{0}$ in fur density and $16^{0}/_{0}$ in the density of the woolly hairs. The juvenile fur and winter fur are similar in the length of the hairs, but show a discrepancy of $39^{0}/_{0}$ in overall density of the fur and as much as $48^{0}/_{0}$ in that of the woolly hairs.

The length, density and colour changes noted here in the harvest mouse in connection with the moult are common to most mammals, and have been shown to be associated with heat regulation. Gorecki

(1966) claims that the winter fur of the bank vole has approximately a $12^{0}/_{0}$ better insulation capacity than the summer fur, while the corresponding difference in the common shrew is $18^{0}/_{0}$ (Gębczyński & Olszewski, 1963).

In the opinion of Traeger (1965) the insulation properties of the fur in most mammals are largely dependent upon density, and in the case of small mammals the principal component of the fur and determining factor for its density is the woolly hair layer. In contrast, Johnson & Hornby (1975) believe that the fine underhairs of the roe deer are of little importance as insulators and that this function appears to be fulfilled by the air contained within the guard hairs, the winter hairs being better insulators as they are thicker and possess large central cavities in which the air can accumulate, and also stand more erect and therefore provide a greater thickness of fur than in the summer. A different pattern of hair thickness is found in small mammals, however, so that the opposite situation is found in the striped field mouse, Apodemus agrarius, with the hairs finer in structure in winter than in summer, while in A. sylvaticus and A. tauricus hair thickness tends to remain constant throughout the year (Haitlinger, 1968).

Borowski (1958) attributes the changes in density of the fur in the common shrew to the reduction in body size noted in winter, but K hateeb & Johnson (1971) maintain that this is not the only reason in the field vole, but that the follicles also increase in number in the autumn, giving increased growth of new hairs. The present results for the harvest mouse lend themselves well to the latter interpretation, with the juvenile fur the least dense and the winter fur the densest (Table 4), the latter often being derived directly from the former as a result of »moulting«, *i.e.* the activation of new follicles, with no intervening summer fur. At the same time the negative correlation between body size and hair density, naturally in each fur type separately, an observation identical to that of Haitlinger (1968) in the wood mouse, suggests that the number of follicles is more or less constant and does not increase with age.

Moulting does not generally occur during pregnancy or suckling. Only five out of the 52 pregnant or suckling bank voles studied by L e h m a n n (1958) were in the process of moulting. The present material contained two pregnant individuals and two suckling, out of which one suckling female showed indications of a moult. The agent for the prevention of moulting is apparently oestrogen during pregnancy and luteotropic hormone during suckling (M o h n, 1958). Thus the difference noted between the active and inactive females in the

frequency of moulting may well be due to hormonal factors. It may then be assumed that the low rate of moulting in October among the female harvest mice must be attributable at least in part to the higher proportion exhibiting sexual activity in autumn by comparison with the males, for it is rare for the males from the late summer broods to achieve sexual maturity by the autumn, while this is more common in the females.

According to Kubik (1952), the harvest mouse in nature winters only once and does not change its fur in the second autumn, a feature which is also detectable in the present results, where those individuals still possessing their summer fur in the autumn had a mean body length of 61.0 mm compared with 56.3 mm for those with their winter fur by the same stage, a discrepancy of 4.7 mm. On the other hand, those with winter fur in midwinter were 1.4 mm longer than those with winter fur in autumn, suggesting that those with summer fur were individuals which had already wintered once and then died as winter approached. The largest, oldest (wintered) specimens identified in the autumn were pregnant and suckling females (Koskela & Viro, 1976), in which the moult would be prevented by hormonal action (see above). This lack of a moult is obviously a protective mechanism to ensure better nutritional reserves for embryo development and suckling of the young, and is thus of significance for the species' breeding success, even though it inevitably leads to the elimination of the breeding females from the population in late autumn.

The high incidence of moulting, among the specimens with winter fur, $41-80^{\circ}/_{\circ}$, throughout the time interval studied, indicates that the harvest mouse may well have an »intermediate coat« of the type described by Haitlinger (1968) for the wood mouse. This may develop directly from the juvenile fur simply by an increase in hair density, principally in the woolly hairs (see above), in which case the length of the juvenile fur, being equivalent to the winter fur, would be ecologically relevant to the preparation for wintering in the juveniles from late summer.

The autumn 0° C isotherm is reached at the end of October or beginning of November in the area from which these individuals were obtained (K olk k i, 1960), permanent snow cover then being established by the end of November or early December (S i m o j o k i, 1960). The majority of the catch from September, 73%, and the entire December material consisted of specimens with their winter fur, which suggests that the autumn moult was taking place »in good time« before the onset of winter, and thus also serves as an indication of the species' successful adaptation to the northern conditions.

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TOPOGRAFIA LINKI, LINIENIE I STRUKTURA SIERŚCI U BADYLARKI

Streszczenie

Zbadano cechy linki, linienie i strukturę sierści u 304 badylarek, Micromys minutus (Pallas, 1778), analizując skórki uzyskane z odłowów prowadzonych w okresie IX - I we wschodniej części centralnej Finlandii. Ze względu na topografię linki wyróżniono u osobników dorosłych trzy typy linki (Ryc. 1), z przewagą doogonowej i dogłowowej (Tab. 1). Jest to cecha różniąca badylarki od innych zbadanych gatunków Muridae, wśród których najpowszechniejszy jest typ dorsalny. Częstotliwość występowania wyróżnionych typów linki nie zależy od płci, typu okrywy włosowej czy sezonu roku. Osobniki w trakcie linki stanowiły 49,3% analizowanego materiału i ilość ich zmienia się w poszczególnych miesiącach. Największy udział zwierząt liniejących notowano w listopadzie (Ryc. 3). U M. minutus wyróżniono 3 typy okrywy włosowej: zimową, letnią i juvenilną (Ryc. 3) i 3 rodzaje sierści (Ryc. 4). Wykazano, że sierść zimowa jest dłuższa od letniej o 9-15%. Sierść osobników młodych jest takiej samej długości jak sierść zimowa, jest jednakże mniej gęsta niż zimowa i letnia. Osobniki z zimowym włosem w 41-80% były w stadium linienia, posiadając pośrednią zimową okrywę włosową. Rozwija się ona z futra juvenilnego, poprzez przyrost włosów wełnistych. Dlatego też długość sierści juvenilnej ma ekologiczne znaczenie dla młodych, urodzonych w końcu lata, jako przystosowanie do zimowania (Tabela 3 i 4). Rzadsza okrywa włosowa uwarunkowana jest mniejszą ilością włosów wełnistych i charakterystyczna jest dla okrywy letniej. Wykazano też negatywną korelację między rozmiarem zwierzęcia a gęstością włosów przypadających na jednostkę powierzchni (Ryc. 5).