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COAT COLOUR INHERITANCE IN AMERICAN MINK (*NEOVISON VISON*): PEDIGREE ANALYSIS

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ABSTRACT

This work aims to establish a simplified genotype for American mink (*Neovison vison*), on the basis of a group of basic genes (*Asip*, *Tyrp1*, *Tyr*, *Myo5a*, and *Mclr*) and three modifying genes (*fawn*, *Ednrb*, and *Kit*). The analysis used pedigrees of 61 females of standard brown, palomino, and silverblue colour variations. The database covered 380 offspring in nine colour variations: brown, silverblue, palomino, brown cross, palomino cross, pearl, pastel, silverpastel, and white. The analysis led to a simplified genotype explaining the principles of inheritance of most common coat colour variations in Polish mink farms. Due to the limited number of animals and the limited number of colour variations used, the analysis could not test the inheritance of all colours found in mink. The genotype was constructed on the basis of the homologous genes responsible for coat colour found in most animal species.

Key words: genotype, homologous genes, coat colour variations, *Neovison vison*

INTRODUCTION

One of the most popular species of fur animals is American mink (*Neovison vison*), valued above all for the excellent quality of fur in various colour variations. In the U.S., mink have been farmed for fur for over a century. The species was brought to Europe at the beginning of twentieth century, the first farms being set up in Germany in 1926. In the thirties of the twentieth century, the interest in mink increased, probably because of the fashion for short haired furs. Mink farming intensified after the second world war. Presently the leading mink-producing country is Denmark, and other major producers include Poland, China, and the U.S. The original wild mink were dark brown, with light brown underfur and big white markings under the chin, on the neck, and on the belly. The first colour variation in mink was silverblue, recorded in 1931. It gained much interest among both breeders and buyers. After this success, breeders became more interested in colour mutations and took greater care of animals other than standard brown. Breeders also tried to understand the mechanism of colour inheritance, which led to creating many interesting colour variations by the end of the twentieth

century. Currently, breeders distinguish over thirty basic coat colours and many different combined variations in this species. The knowledge of its coat colouration inheritance, however, is still scarce, partly because of the unique naming system used for genes responsible for coat colour in American mink [Nes et al. 1988, Kuźniewicz and Filistowicz 1999].

The paper aims to analyse the coat colour inheritance of American mink on the basis of pedigree analysis. To this aim, analogue genes responsible for coat colour of American mink will be determined. Because of the limited number of colour variations in the sample, it was impossible to determine the full set of genes responsible for coat colour. This study might help to simplify the current classification of coat colour in American mink and to find relationships between different colour variations in this species.

MATERIAL AND METHODS

Pedigree base

The study used the pedigrees of sixty-one females born in 2015 in a small farm located in the Greater Poland

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Voivodeship (Wielkopolska Voivodeship), Poland. The pedigrees were established using their breeding cards, supported by consultations with the farm owner whenever needed. Most females had pups in several colour variations, and only several had all pups of the same coat colour as their mothers. The study involved three variations: standard brown (41 females), palomino (8 females), and silverblue (4 females). They were mated with males of the following colour variations: palomino, pearl, cross palomino, standard brown, silverblue, and aleutian silver (sapphire). This gave 380 pups in nine colour variations, determined on the basis of phenotypic evaluation conducted by one of the authors (P.W.) and the farm owner: standard brown (174 pups), silverblue (103), palomino (66), cross brown (10), cross palomino (8), pearl (6), ambergold pastel (4), pastelsilver (3), and white (2).

The females and their offspring were divided into seven colour groups. These groups were then divided into subgroups on the basis of colour variations of the males with which the females were mated. The resulting classification is presented below.

1. Standard brown females with standard brown, palomino, pastel, and cross palomino offspring (13 females with 80 pups):
 - mated with pearl males,
 - mated with palomino and palomino cross males,
 - mated with standard brown males.
2. Standard brown females with standard brown, silverblue, and ambergold offspring (24 females with 158 pups):
 - mated with silverblue males,
 - mated with palomino and palomino cross males,
 - mated with pearl males,
 - mated with standard brown males.
3. Standard brown females with standard brown, palomino cross, and brown offspring (4 females with 22 pups):
 - mated with palomino and palomino cross males.
4. Standard brown females with standard brown, palomino, silverblue, and pearl offspring (5 females with 34 pups):
 - mated with pearl males,
 - mated with palomino males.
5. Palomino females with palomino, pearl, palomino cross, pastelsilver, and white offspring (8 females with 45 pups):
 - mated with pearl males,
 - mated with palomino males.
6. Silverblue females with silverblue offspring (4 females with 27 pups):
 - mated with silverblue or sapphire males.

7. Standard brown females with standard brown offspring (3 females with 14 pups):

- mated with standard brown males.

Methods

First, coat colour inheritance in other mammalian species was analysed in terms of genes responsible for main coat colours similar to coat colours typical of American mink. On the basis of this analysis, several hypotheses about a possible mink genotype were proposed and verified using pedigree analysis.

The pedigrees went back two or three generations. For each female, its pedigree included the following information: the number of pups, splitting of colour variations, an ID number, coat colour, and IDs and colour variations of the males it mated with. In American mink, it is practically impossible to establish paternity with certainty, due to common multiple mating (with different males) in mink breeding and the resulting possibility of female insemination by more than one male [Shackelford 1980, Yamaguchi et al. 2004, Felska-Błaszczuk et al. 2019, Seremak et al. 2020]. If the pedigree included information about grandfathers and great-grandfathers, only their coat colour variations were used in the analysis. All the animals analysed were assigned the genotype which corresponded to its colour variation.

The research was carried out in two stages. In the first one, the genotypes of the animals analysed were determined, in accordance with the applicable nomenclature. However, to facilitate the interpretation of the genotypes, they were shortened by rejecting alleles repeated in every coloured variation among the pedigrees studied. Since the Swedish palomino, the Finnish palomino, and the Swedish albino coat colours are impossible to distinguish by eye, one allele (t) was assumed for all the palomino variations.

The second stage of the research aimed to find analogous genes that could be responsible for the colour variations present in the database.

RESULTS

Table 1 shows the genes that can be responsible for various colour variations in American mink, selected on the basis on the pedigrees analysed and literature data.

The loci used in the genotypes were proposed due to the spectrum of their activity known for other mammalian species. The genotypes represent the final version of the hypotheses tested on the data sample collected from the pedigrees. Since the animals were assigned to the appropriate colour variations using the phenotypic evaluation, there is a possibility of incorrect classification of some individuals.

Table 1. The simplified genotypes of colour variations in American mink

Tabela 1. Uproszczone genotypy odmian barwnych norki amerykańskiej

Standard brown	aa	B ₋	C ₋	D ₋	F ₋	P ₋	ss
Pastel	aa	bb	C ₋	D ₋	F ₋	P ₋	ss
Palomino	aa	bb	C ₋	dd	F ₋	P ₋	ss
Pearl	aa	bb	C ₋	dd	ff	P ₋	ss
Silverblue	aa	B ₋	C ₋	dd	F ₋	P ₋	ss
Aleutiansilver	aa	B ₋	C ₋	dd	ff	P ₋	ss
Pastelsilver	aa	bb	c ^e c ^e	dd	F ₋	P ₋	ss
White	aa	—	c ^e c ^e	—	—	Pp	ss
Cross	aa	B ₋	C ₋	D ₋	F ₋	P ₋	S ^c ₋

Underscore “₋” means it is irrelevant whether the allele is of the same or lower dominance in the series.

Symbol „₋” oznacza dowolność występowania alleli takich samych lub będących niżej w szeregu dominacji.

The pedigrees analysis showed that the majority of brown females had ancestors of various colour variations. Of the 49 females, only 19 came from the pure standard brown variation; 16 had an ancestor of the palomino variation, and 10 had an ancestor of the silverblue variation. For four females, it was impossible to determine the exact coat colour of their ancestors, because their mothers mated with males of different colour variations (but not standard brown). The diversity among pups and females’ ancestors suggests that currently mink breeders do not pay too much attention to keeping the purity of colour lines. Similar conclusions can be drawn on the basis of the distribution of coat colour in the offspring of the females not included in this study due to the inability to determine their pedigrees.

The genotypes

Till now, the colour agouti (in which a hair displays alternating bands of dark and light pigmentation) has been reported in none of the colour variations discussed, suggesting that domesticated mink, both wild type and colour type ones, represent a non-agouti variation [Searle 1968, Bennett and Lamoreux 2003, Cieslak et al. 2011]. Although the standard coat colour is divided into blue and brown standards, they are represented by the same genotype. In the genotypes proposed, the *B* allele is considered responsible for the standard brown variation, due to the dark-brown hair – close to black – the allele is associated with. The recessive *b* allele is likely responsible for the pastel variation. Since this variation has quite a few colour mutations, the *Tyrip1* locus can be assumed to contain a number of multiple alleles determining various pastel variations [Searle 1968, Schmidt-Küntzel et al. 2005, Cieslak et al. 2011, Cirera et al. 2016, Cai et al. 2017].

The dominant allele of the *Tyr* gene, responsible for normal pigment production, has occurred in most animal species studied for coat colour [Schmidt-Küntzel et al. 2005, Cieslak et al. 2011]. Mink considered to be albino are actually not pure white. Their coat has pigmented ar-

eas, most often in the distal parts of the body [Nes et al. 1988]; thus, the *c* allele can be excluded from the candidate genes responsible for the white coat of the mink. The albinopastel variations may be due to the interaction of the *c^ec^e* (extreme dilution) and *pp* (pink-eyed dilution) alleles, whose combination results in animals with pink eyes and a pure white coat [Searle 1968, Cieslak et al. 2011, Ruvinsky and Sampson 2001].

The action of the *Myo5a* gene has been quite well understood in other mammalian species, such as dogs, cats, mice, and rabbits [Searle 1968, Desnos et al. 2007, Fontanesi et al. 2012]. Some of these species have variations with brightened coat colour phenotypically similar to colours of mink, for example Russian blue in cats or Isabella in dogs – hence the decision to include the *d* allele in the genotypes.

The interaction of the *dilution* and *fawn* genes has been proposed responsible for the sapphire and pearl variations, due to a similar interaction effect these genes have in rats. These coat colours were considered “doubly” recessive, like caramel, taupe, and peach in cats [Searle 1968, Ruvinsky and Sampson 2001]. Many studies conducted over a long period on colour variations in mink have proved the dominance of frosted variations over uniform ones. The database analysed confirmed this rule, suggesting including in the genotype the *S* gene – also occurring in cats – which determines the dominant white spotting [Searle 1968, Schmidt-Küntzel et al. 2005, Cieslak et al. 2011, Cai et al. 2017]. The cross variation was marked as *S^c* (white spotting-cross).

Pastelsilver raised the greatest doubts among the colour variations, because the three pastelsilver pups had palomino mothers and pearl fathers. In these cases, the pups’ colour may result from the overlap of two brightening genes (*c^ec^e* and *dd*) with different spectra of activity (the *Tyr* gene regulating melanogenesis and the *Myo5a* gene being responsible for transporting melanocytes). Because a phenotypically similar variation had not appeared in this breeding farm previously, it is also possible that it was incorrectly classified.

DISCUSSION

Attempts to determine American mink's genotype began with the appearance of new colour variations in breeding. A pioneer in this field was Richard M. Shackelford, who published back in 1941 the article "Mutations in mink" [Shackelford 1941]. Until 1980, more than 25 genes were discovered whose mutations affect coat colour in mink; a new terminology had thus to be constructed for mink genotype [Shackelford 1980]. The book "Comparative Genetics of Coat Color in Mammals", by Antony G. Searle, assigns individual coat colour genes to appropriate gene groups, maintaining the terminology used for mink. The book describes all basic colour variations known at the time and mentions several important variations of colour combination [Searle 1968]. Searle assigned brown standard, considered the most basic colour, to the group of *B* genes. The present work assumes that standard brown is determined by the dominant *B* allele. However, since the standard variation is divided (mostly by researchers, but not necessarily by breeders and action houses) into blue and brown standards, it does not reject the possibility of existence of modifying genes or of an allele determining a darker shade of brown. A similar situation occurs in mice, in which a dark brown cordovan coat is determined by the *b^c* allele. Searle excludes the occurrence of pheomelanin in mink, in contrast to Shackelford, who found it to occur in palomino variations [Searle 1968, Shackelford 1980]. This study did not cover variations with reddish or yellowish colours, such as glow or amber, so the occurrence of pheomelanin was not studied. Palomino mink usually have coat colour in the shade of beige or cream, suggesting that this variety be assigned as brightened pastels and that it belongs to brown colour coat variations. Cirera et al. [2016] recently suggested that an insertion in *Tyrp1* gene is responsible for several brownish phenotypes, including some of the palomino family.

According to a study by Anistoroaei et al. [2011], mutations in the *extension* gene are likely involved in the formation of pastel, pearl, palomino, and glow-type coat colour variations. Searle, on the other hand, qualified some of the pastel variations (i.e., royal, imperial, amber gold, and green-eyed pastels) to the group of *B* genes. He considered mutations within the *C* gene responsible for the Socklot pastel and the other variations determined by the *t* allele series. Unfortunately, since the database analysed included only a few American mink with pastel coat colours, it was impossible to thoroughly test the inheritance of pastel variations. The research by Shackelford [1948] into the variation in the shape and orientation of melanin grains showed their irregular distribution in the silverblue variation and the accumulation of pigment mainly in the hair medulla. This phenomenon may result from the action of the *Myo5a* gene, analysed in this study,

confirming the theory that this gene is involved in the formation of blue variations. Searle also included the allele *p* series (responsible for the steelblue and silverblue variations) in the *dilution* gene group [Searle 1968]. Recently, Cai et al. [2017] constructed a draft genome sequence for American mink and confirmed that the mink genome includes several genes considered in the present study, such as *Asip*, *Mcl1r*, *Kit* and *Tyr*.

CONCLUSIONS

The results represent only a small part of the complete mink genotype, the knowledge of which would enable one to explain the rules governing the inheritance of coat colour, one of the most important functional features of fur animals. Due to the limited number of animals and colour variations in the database analysed, inheritance methods could have been tested only for the ten colours found in the pedigrees (standard brown, silverblue, palomino, brown cross, palomino cross, pearl, pastel, silverpastel, white, and sapphire).

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DZIEDZICZENIE BARWY OKRYWY WŁOSOWEJ U WIZONA AMERYKAŃSKIEGO NA PODSTAWIE ANALIZY RODOWODÓW

STRESZCZENIE

W pracy podjęto próbę ustalenia uproszczonego genotypu dla wizona amerykańskiego (*Neovison vison*), w oparciu o grupę genów podstawowych (*Asip*, *Tyrp1*, *Tyr*, *Myo5a*, *Mc1r*) oraz kilka genów modyfikujących (*fawn*, *Ednrb*, *Kit*). Analizę przeprowadzono na podstawie bazy danych składającej się z rodowodów 61 samic odmian standard brązowy, palomino i silverblue. Głównym obiektem badań było 380 młodych w 9 odmianach barwnych: standard brązowy, silverblue, palomino, cross brązowy oraz palomino, perła, pastel, silverpastel, białe. Uzyskane wyniki stanowią uproszczony genotyp wyjaśniający schemat dziedziczenia najczęściej występujących w polskich hodowlach odmian barwnych norki. Genotyp skonstruowany został w oparciu o występujące u większości gatunków zwierząt geny homologiczne odpowiadające za barwę okrywy włosowej. Ze względu na ograniczoną liczbę badanych zwierząt oraz występujących w rodowodach odmian barwnych niemożliwe było dokładne przetestowanie dziedziczenia wszystkich występujących u nerek umaszczeń.

Słowa kluczowe: genotyp, geny homologiczne, odmiany barwne, *Neovison vison*