

Preliminary studies on the inheritance of white coat colour in Arctic foxes (*Alopex lagopus* L.)

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Abstract. Main genes determining white coat colour in Arctic foxes are: recessive gene *d* and incompletely dominant, autosomal gene *S* with lethal effect in homozygous condition. The white coat colour of Arctic foxes bred on Polish farms had been determined solely by the recessive gene until the 1970s, when the Shadow variety was imported from Norway. The genetic code of the two varieties was different, but this fact was not taken into account. The results obtained in the present study do not confirm the theories on the heredity of white coat colour of Arctic foxes. The authors of these theories assumed that the coat colour depends on the presence of a recessive gene, the only factor responsible for the white furcoat. Apart from Polar and Shadow white foxes, there is a wide variety of darker white animals, and this fact suggests that there is a number of cumulative genes responsible for the intensity of coat pigmentation.

Key words: Arctic fox, blue type, coat colour, inheritance, white type.

Introduction

The knowledge of the inheritance of white coat colour of Arctic foxes is still inadequate. Many researchers (SLAGSVOLD 1949, JOHANSSON 1960, LOHI 1985, JEŻEWSKA et al. 1987, NES et al. 1988) are in favour of the theory that the dark colour of Arctic foxes dominates over the white. This suggests that white individuals are always recessive homozygotes (LOHI 1978) and mated together should produce only white offspring.

The polar fox is the most common white type of Arctic foxes. According to the Scandinavian gene symbols for colour types of the Arctic fox (LOHI 1985), the coat colour depends on the presence of the recessive gene *d* (SLAGS-

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VOLD 1949). In the American gene symbols for colour types of the Arctic fox the recessive gene has been assigned the symbol *bl* (SHACKELFORD 1982). Polar foxes are white or almost white in winter, but in summer the colour turns brownish grey, from pale to dark, depending on the part of the body and age of the animal. Completely white individuals are rather scarce, since the underfur of the majority is bluish. This suggests that the resulting coat colour is due to the interaction between the polar genes and genes affecting the darkness of the coat.

The Albino fox is another type of the Arctic fox. Its coat colour is affected by the recessive gene *c* (LOHI 1985). However, this type is hardly ever found, therefore its significance on breeding farms is negligible.

The Shadow fox is a mutant that appeared on a Norwegian farm about 1950-1952. According to NES (1975b), the characteristic of this variety is a large variation in pigmentation, from white to a dark colour resembling that of the dark Blue fox. All adult individuals have slightly coloured ear edges, while the homozygous white Polar fox has completely white ears due to the recessive allele *d*. The Shadow fox is the first of the three Norwegian mutants belonging to the *shadow series* (NES et al. 1988). The shadow colour phase is caused by an incompletely dominant, autosomal gene *S* with a lethal effect in homozygous condition (NES 1975a). According to JEŻEWSKA et al. (1983), irrespective of the gene in locus *S*, there is a pair of unidentified cumulative genes determining the pigmentation of Shadow foxes.

The Aspas White is another mutant affected by the dominant, autosomal gene S^A , which like the gene of the shadow types has a lethal effect in homozygous condition (NES, FUGNER 1984). This mutant appeared on a Blue fox farm in the 1980s, but up to the present day it has not been imported to Poland.

The white coat colour of Arctic foxes bred on Polish farms had been determined solely by the recessive gene until the 1970s, when the shadow variety was imported from Norway. The genetic code of the two varieties was different, but this fact was not taken into account (JEŻEWSKA et al. 1987). The imported animals were preferred in reproduction because of their pelage, considered superior to that of the Polish breeding material. In this way, the frequency of the recessive genes responsible for white colouring has been reduced, while the frequency of the dominant genes of the shadow variety, which in homozygous condition have a lethal effect, increased. Generally, the Shadow foxes bred in Poland are white with a dark shadow formed by pigmented tips of some guard hairs (CHOLEWA, GEDYMIN 1974).

The purpose of the present study was to determine the frequency of coloured varieties of progeny resulting from different matings of blue and white foxes.

Moreover, we made an attempt to verify the hypothesis on the inheritance of white coat colour of Arctic foxes.

Material and methods

The material taken for the study consisted of animals whose parents were of well-known genealogy and coat colour. The analyses comprised the data collected in the years 1984-1994 and they were carried out at two stages; first with respect to particular years, and next the total data were analysed, irrespective of the years. The offspring were filed in the Farm Book (1984-1988) and the computer database (1988-1994) LISY (CHUDOBA et al. 1988). The data included: the coat colour of parents and offspring and the heritage of progeny. The data in the Farm Book were considered reliable enough, therefore they were not verified. The data filed in the database were automatically verified by the computer program, i.e. father was excluded if mother had been mated with at least two males during the heat. The analyses comprised the animals after blue \times blue, blue \times white and white \times white parents. The frequencies and the mean number of weaners per litter were calculated for each type of mating. The data were analysed statistically (analysis of variance, SAS/STAT USERS GUIDE 1988) in order to determine the effect of the type of mating and the years on the mean litter size and the number of males and females in a litter. Theoretical expectations were compared with the results obtained, using a chi-square test.

Results and discussion

The analyses included 1469 matings of white and blue foxes. All animals belonged to the foundation stock which met the requirements of the investigation, i. e. the genealogy of the progeny, both on the father and mother's side (father was the only sexual partner of the female) was well-documented and so was the coat colour.

The types of mating are shown in Table 1. As can be seen, the most common was blue \times blue mating (\times 1286) which gave 9841 weaners. Blue foxes were mated with white individuals 117 times, including blue males with white females (\times 90) which gave 719 weaners, and white males with blue females (\times 27) which gave 210 weaners. White foxes were mated 66 times and produced 375 weaners. It was found that the litter size depended on the type of mating. The mean values (Table 1) of the litter size noted in the group of blue parents (7.50 weaners), blue male \times white female (7.86 weaners), or white male \times blue female (7.78 weaners) do not show significant differences, but the mean litter size noted in the group of both white parents (5.59 weaners) is markedly lower.

The litter size of white parents was 25% lower than that observed in the groups of blue or blue \times white parents. This suggests the presence of a dominant, lethal gene *S* (responsible for the white coat) in the population of Arctic foxes examined in the study. Gene *S* in homozygous condition causes the death of 25% of the embryos, hence the reduction in the litter size of white \times white matings. The genes in locus *W* have a similar impact on silver foxes (BELYAEV et al. 1973, 1975), where the lethal effect also occurs at the embryonic stage of the ontogeny. The data presented in Table 1 confirm a high frequency of gene *S* and a low percentage of recessive genotypes responsible for the white colour, since during the observation period (1984-1994) only 0.1% of white foxes and 99.9% blue individuals had blue parents, the potential carriers of the recessive gene *d* responsible for the white coat.

JEZEWSKA et al. (1987) drew similar conclusions, finding that on those Polish farms, where white \times white foxes were mated, the reductions as compared with the other types of mating, averaged 2.7 pups at birth and 1.7 weaners. These data confirm a high frequency of the genes responsible for the shadow colour in the population of white-coated Arctic foxes bred on Polish farms.

Table 1. Number of litters (M), litter size (n), frequency (%) of white and blue offspring in relation to coat colour of their parents

Type of mating		M	n	Coat colour of offspring (%)	
male	female			blue	white
Blue	Blue	1286	7.50 a	99.9	0.1
Blue	White	90	7.86 a	53.6	46.4
White	Blue	27	7.78 a	55.3	44.7
White	White	66	5.59 b	38.5	61.5
Total		1469	7.44	93.7	6.3

Common letters indicate means not differing significantly at $P = 0.05$.

The litter size of blue \times white parents (Table 1) was in each case significantly larger than that resulting from white \times white and slightly larger than that of blue \times blue matings. The number of weaners resulting from the matings of white males \times blue females (Table 1) was 7.78, while 7.86 weaners were obtained when blue males had been mated with white females. Although the litter sizes slightly increased in the case of blue \times white matings, the increase was insignificant as compared to the matings of blue foxes. On the other hand, the difference suggests a higher survival rate of the hybrids resulting from blue \times white matings.

The majority (99.9%) of blue parents' offspring were blue in colour, while only 0.1% were white (Table 1). The average litter size of blue pups (Table 2) was 7.48 pups per litter, which was significantly higher than that of the remaining three types of mating. In contrast, the number of white pups (Table 2) which averaged 0.02 per litter, was significantly lower than that of white foxes resulting from the other three types of mating. This means that the majority of blue foxes are homozygous and contain the genes responsible for the blue coat colour. The white pups born here and there suggest that both males and females must be heterozygous carriers of the recessive gene *d* responsible for the white colour of the coat.

Table 1 shows that 53.6% of blue offspring were produced by mating blue males with white females (46.4% of pups were white). A similar situation was observed when white males had been mated with blue females (55.3% of the offspring were blue and 44.7% white). If we assume that in either type of mating, white parents were carriers of the shadow gene *S*, and blue parents were homozygous (*ss*), then the percentage of pups different in colour is neither significant (blue males \times white females $\chi^2 = 3.73 < \chi_{0.05}^2 = 3.84$, white males \times blue females $\chi^2 = 2.36 < \chi_{0.05}^2 = 3.84$), nor discrepant from the theoretically expected 1:1 ratio.

The litter size of blue pups produced by a white male and blue female averaged 4.30, or 4.21 pups per litter when the male was blue and female white. These differences are not significant, but those between the litters produced by blue or white parents only, were pronounced.

In 66 litters of both parents white in colour (Table 1), 38.5% of pups were blue and 61.5% white. The number of blue pups in a litter averaged 1.95 and was significantly different from the mean number of blue pups obtained in the other types of mating. The mean litter size of white pups (3.64 per litter) was significantly different from that observed when both parents were blue. These data suggest that some white foxes die at the embryonic phase, since the mean number of litters obtained from such types of mating (Table 1) accounted for 75% of either blue or blue \times white fox litters. The expected ratio of white to blue pups was 3:1 and the ratio obtained in our study was 1.5:1 (Table 1). The difference is statistically significant ($\chi^2 = 36.45 > \chi_{0.01}^2 = 6.63$).

No effect of the type of mating on the sex of animals in a litter was observed (Table 2). A significant difference between the number of males and females in the litters of white parents and the litter size (both sexes) of the remaining three types of mating was observed. This was due to the reductions in the litter size caused by the lethal gene, resulting in a smaller number of pups of both sexes.

Table 2. Mean number of blue and white, male and female pups in litters resulting from 4 different types of mating

Type of mating		Number of pups per litter		Sex of offspring	
male	female	blue	white	male	female
Blue	Blue	7.48 a	0.02 a	4.02 a	3.48 a
White	Blue	4.30 b	3.48 b	4.37 a	3.41 a
Blue	White	4.21 b	3.65 b	3.99 a	3.87 a
White	White	1.95 c	3.64 b	3.01 b	2.58 b
Total		6.97	0.47	3.97	3.47

Common letters indicate means not differing significantly at $P = 0.05$

In 1984, white foxes were not mated together in order to avoid the reductions in the litter size. According to the data in literature and breeders' opinions, this type of mating is responsible for the reductions in the litter size, due to the presence of the lethal gene in some populations of white foxes. A growing demand for the pelts of white Arctic foxes on the market caused the fact that a year later (1985) four attempts were made to mate white foxes again. The number of matings in the following years was: 18 in 1986, 21 in 1987 and 18 in 1988. The mean number of litters produced by white parents was significantly lower than that of three other types of mating in 1988, therefore, in 1989 the number of white \times white matings was limited to four and in 1990 to a single one. No white \times white foxes were mated in the years 1991-1994.

Each year the number of weaners from the litters of white parents was markedly lower as compared to the litters of other groups of parents. In the years 1985-1990 the litter sizes of white parents were as follows: 5.5, 5.9, 6.1, 5.4, 4.5 and 1.0 pups per litter, respectively. Since there was only one mating in 1990, the last value should not be taken into account. The first and last but one values were obtained in 1985 and 1989 when the matings of white \times white foxes took place only four times, therefore, these data should not be considered fully reliable, either.

In the years when white \times white foxes were mated together, an average litter size of blue pups significantly decreased, while the mean number of white pups increased. This tendency was particularly clear in 1987 (5.81 blue and 1.46 white pups in a litter) and 1988 (5.37 blue and 1.41 white pups in a litter). A declining tendency in the mean number of weaners (Table 3) was observed in 1985-1990 when the mating of white foxes was quite common. In 1984 there were 9.04 pups at weaning, 8.05 in 1985, 6.93 in 1986 and only 4.56

Table 3. Number of matings (N), mean number of weaners, blue and white pups per litter

Years	N	Mean number of pups per litter		
		total	blue	white
1984	70	9.04 a	8.76 a	0.28 dc
1985	61	8.05 b	7.51 b	0.54 bcd
1986	76	6.93 c	6.09 dc	0.84 b
1987	75	7.27 bc	5.81 d	1.46 a
1988	86	6.78 cd	5.37 d	1.41 a
1989	63	5.92 d	5.19 d	0.73 bc
1990	46	4.56 e	4.09 e	0.47 bcd
1991	81	7.30 bc	7.17 b	0.13 d
1992	161	7.25 bc	7.03 bc	0.22 d
1993	391	8.03 b	7.73 b	0.30 cd
1994	359	7.43 bc	7.14 b	0.29 cd
Total	1469	7.44	6.97	0.47

Common letters indicate means not differing significantly at $P = 0.05$.

in 1990. This was likely due to the less efficient reproduction of white parents followed by the reductions in average litter sizes.

Conclusions

The results obtained in the present study do not confirm the theories on the heredity of white colouring of Arctic foxes. The authors of these theories assumed that the coat colour depends on the presence of a recessive gene, the only factor responsible for the white furcoat. Now, we know that pale shadow foxes can also be referred to as white, but the colour of their pelage is affected by gene *S* which has a lethal effect in homozygous condition. Apart from shadow white foxes, there is a wide variety of darker shade animals, and this fact suggests that apart from gene *S*, there is a number of cumulative genes responsible for the intensity of coat pigmentation.

Analysing the frequency of white and blue progeny of white, blue and white \times blue mates, the following conclusions can be drawn:

1. There are two different genes responsible for white pelage in the population of Arctic foxes, subjects of the present study:
 - a) a recessive, non-lethal gene (common in foxes bred in Poland in the 1960s, but at present very rare);

b) a dominant gene (imported from Norway with shadow foxes in the 1970s) which has a lethal effect in homozygous condition.

2. White foxes are either homozygous (the recessive, non-lethal gene) or heterozygous (the dominant, lethal gene).

3. Reductions in the litter size (75% as compared to other types of mating) resulting from the mating of two white foxes suggest that 25% of embryos die because of the lethal effect of the shadow gene.

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