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THE ISSUE OF BLUE DUN SHADE INHERITANCE IN THE HORSE

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ABSTRACT

The blue dun colour shade is not a selection criterion in Polish Konik horse breeding, hence it has been possible to undertake the analysis of its inheritance on the example of this population. The material consisted of Polish Konik horses registered in the Studbook.

The percentage of variously shaded horses has remained at similar level since the horses recorded in the 5th volume of the Stubook. Different mating types with regard to the shade have resulted in progeny of three blue dun shades: standard, light and dark. The distributions of variously shaded progeny from these matings differ which suggests that the blue dun shade depends on the horse genotype. The numbers of different shades in males and females are alike. The results indicate that the blue dun colour shade may be controlled by *E* and *D* loci in the way that dominant *E* allele darkens the shade and dominant *D* allele lightens it, though they are not equally effective.

Key words: blue dun colour, shade, inheritance, Polish Konik, horse.

INTRODUCTION

The Polish Konik horse derives from Tarpans, which were blue dun. This coat colour was probably the protective colouring helping the horses to survive under harsh environmental conditions [7]. Since the beginning of breeding, the Polish Konik horse has been to remind the most its wild ancestors. Hence, it has been selected for the blue dun coat colour without white markings. However, the selection criteria have never concerned the colour shade and light, standard (in Polish literally called blue dun), dark and yellow shaded blue dun horses have been accepted in the breeding [5]. It should be mentioned that in the world the blue dun shades are also distinguished otherwise. This may result among others from the activity of additional alleles present in various populations, e.g. the *Cremello* allele. In the light of hitherto studies, the blue dun shade in a horse seems to be a constant property, in spite of some fluctuations in the hair colour which occur according to the season of the year [6, 10, 12] and the horse's age [7, 9, 10].

The blue dun coat colour appears in the horse of *aaE_D_* genotype [1, 2, 3, 4, 13]. Matings of heterozygous blue dun horses may produce *aaE_dd* black foals, _ _*eeD_* red dun foals and _ *eedd* chestnut foals [2, 3, 9]. In Polish Konik Studbook, both red dun horses and rare chestnut horses have been recorded as chestnuts and therefore it is not possible to distinguish the two colours in them. Dominant *A* allele present in e.g. dun *A_E_D_* horses, does not occur in the population any more [11]. The blue dun shade inheritance has not been still discovered, perhaps because of the lack of sufficiently numerous blue dun horse populations in the world. As it is known, the blue dun colour occurs in some primitive horse breeds but is a breed property only in the Polish Konik. Former study including 127 Polish Konik matings showed that the blue dun shades could be determined by two sex-limited genes [9]. However, the suggested inheritance model was not sufficiently documented.

The objective of the study was to try to define the blue dun shade inheritance on the example of the Polish Konik population.

MATERIALS AND METHODS

The study was conducted on Polish Konik horses registered in eight Studbook volumes published up to the present. The shade in 1 107 blue dun horses was considered. 1 066 horses whose parents were of known colours were included in the genetic analysis. These were both blue dun (n=1 016) and non-blue-dun horses (n=7) resulted from blue dun horses mated *inter se*, as well as horses of various colours produced in blue dun x non-blue-dun matings (n=43).

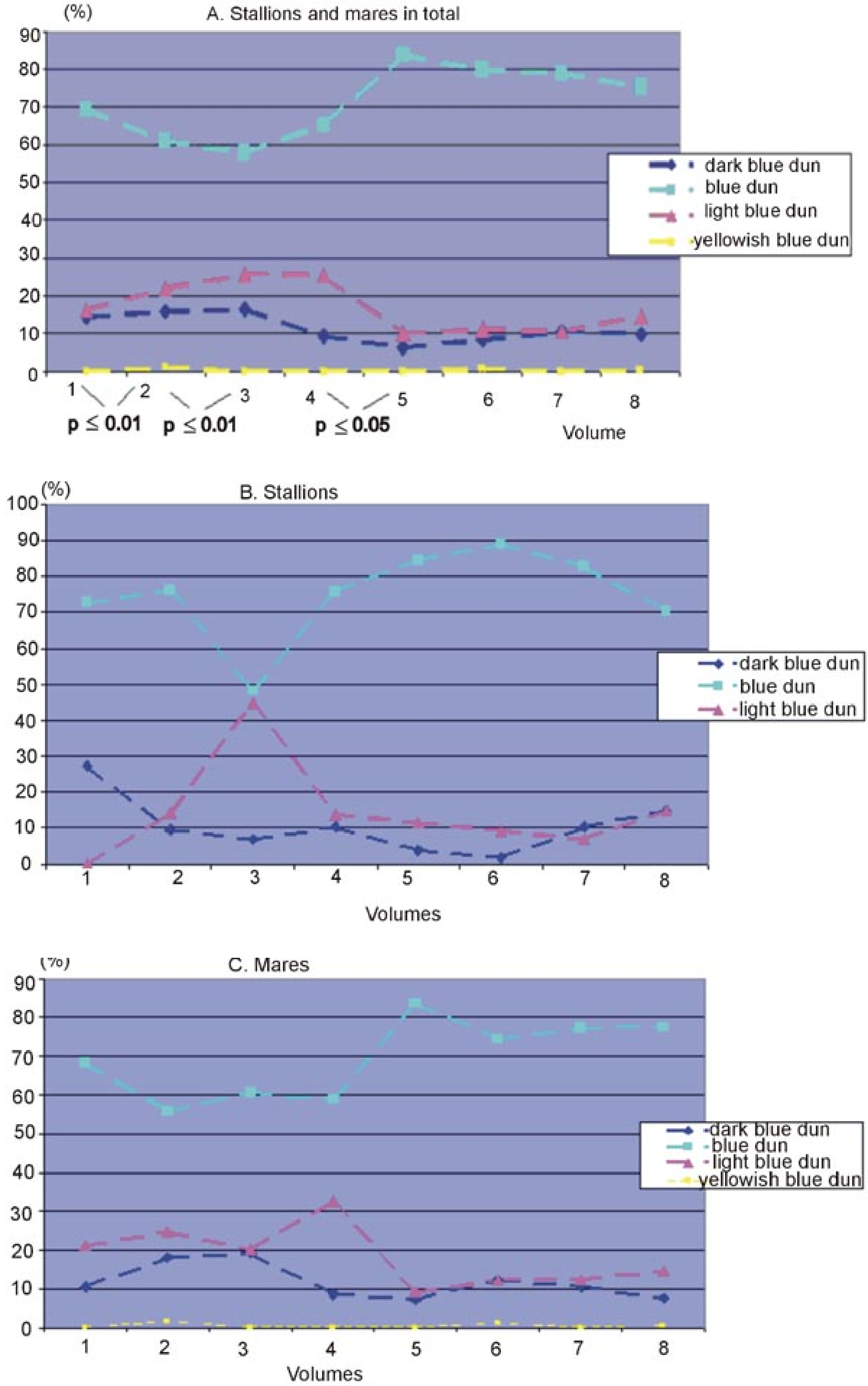
The changes of the blue dun shade percentage in the Polish Koniks were analysed between the successive volumes of the Stud Book. The shade segregation ratio was studied in foals produced in various types of matings. The yellow-shaded-blue-duns which occur very rarely (n=3), were excluded from the analysis. The alleles present in *A* locus were not considered, since all individuals were assumed to be of *aa* genotype [11].

The shade distributions were compared with the use of chi^2 test, provided the horse number was sufficient. The expected phenotype frequency in the population was estimated on the basis of allele frequency in 514 Polish Konik horses present in the breeding herd in 2002 [11].

RESULTS

Most of the Polish Konik horses were of the standard shade (73.1%), fewer were light blue dun (15.8%) or dark blue dun (10.8%). Solely in the 3rd volume of the Studbook almost half of the stallions was light blue dun (Fig. 1A, B and C). The yellow-shaded-blue-duns were rare (0.3%). The percentage of variously shaded blue dun horses changed significantly in the first three volumes of the Book ($p \leq 0.01$) and between the 4th and 5th volumes ($p \leq 0.05$). The standard horse percentage lowered at the beginning, then increased over 80% in the 5th volume and insensibly decreased again. It can be generally stated that the number of variously shaded blue dun horses has been remaining at a similar level since quite a long time.

Fig. 1. Percentage of Polish Konik horses registered in the Studbook



The distributions of the three blue dun shades in offspring produced by blue dun parents are presented in Table 1. Foals of all three shades derived from particular kinds of matings and only few dark horse *inter se* matings did not result in light shaded foals. The latter is not consistent with the observations by Kownacki [7] who stated that in Polish Koniks sometimes light foals appeared from both dark shaded parents. They could have been only individuals not registered in the Stud Book or, what is less possible, recorded with mistakenly described shade. Hence, such cases, if ever happen, are rare.

Table 1. Blue dun shade distribution in Polish Konik horses produced in various kinds of matings

Parents	Progeny								
Kind of mating	dark		standard		light		total		difference significance between ratios
	n	%	n	%	n	%	n	%	
Dark x dark	5	83.3	1	16.7	0	0.0	6	100.0	
Dark x standard	26	25.0	71	68.3	7	6.7	104	100.0	AB
Dark x light	1	3.8	21	80.8	4	15.4	26	100.0	
Standard x standard	62	10.9	443	78.1	62	10.9	567	100.0	AC
Standard x light	8	3.1	176	69.3	70	27.5	254	100.0	BC
Light x light	2	3.4	36	61.0	21	35.6	59	100.0	
Total	104	10.2	748	73.6	164	16.1	1016	100.0	

The distributions of variously shaded blue dun horses marked with the same letters significantly differ at $p \leq 0.01$.

Dark shaded horses mated to standards also produced a low percentage of light shaded foals (6.7%) and mated to light shaded horses produced only one dark foal. In the offspring derived from *inter se* standard horse matings, the segregation ratio of dark, standard and light foals was symmetrical: 1:7:1. The lights x standards and lights x lights matings resulted in a very low percentage of dark offspring (3.1% and 3.4%, respectively). In general, dark horses mated to lighter and lighter horses were producing fewer and fewer dark foals and more and more standards and lights. Likewise, standards mated to standards and lights, as well as lights mated *inter se* were producing fewer and fewer dark and standard foals and more and more light foals. Thus, a distinct tendency appears the darker the parents the darker the progeny, and vice versa: lighter parents produce lighter progeny. The significant differences ($p \leq 0.01$) show that the dark, standard and light shades genetically differ which is in agreement with hitherto foundings [9].

Regarding the sex in the parents and foals it should be noted that dark sires did not sire light colts, whereas dark dams gave birth to single light foals of both sexes (Table 2). Simultaneously, the dark sires produced a little bit more dark daughters (35.7%) than the dark dams (23.3%) did and the light dams foaled more light progeny of both sexes than light sires did (Table 3). It could be concluded that the dark sires marked their offspring with the dark shade character more distinctly than dams, whereas the dams transferred the light shade more easily, though the differences were not significant ($p > 0.05$). Besides, there is a visible tendency of a greater percentage of dark daughters than dark sons, produced by dark sires or dark dams. Likewise, light sires and light dams produced relatively a little more light daughters than light sons. It could be concluded that the daughters easier inherited the parental shade than the sons did. Although the significance of these tendencies could not have been statistically documented ($p > 0{,}05$), they do not seem accidental. They are particularly pronounced compared to almost identical shade segregation ratios in sons and daughters of standard sires, as well as in sons and daughters of standard dams.

Table 2. Blue dun shade distribution in Polish Konik horses produced in various kinds of matings with regard to the sex

Parents		Progeny															
		stallions							mares							total	
sire	dam	dark		standard		light		Σ	dark		standard		light		Σ		
		n	%	n	%	n	%	n	n	%	n	%	n	%	n	n	%
Dark	dark	2	100.0	0	0.0	0	0.0	2	3	75.0	1	25.0	0	0.0	4	6	0.6
	standard	2	12.5	14	87.5	0	0.0	16	11	36.7	15	50.0	4	13.3	30	46	4.5
	light	0	0.0	0	0.0	0	0.0	0	1	12.5	6	75.0	1	12.5	8	8	0.8
Standard	dark	3	16.7	13	72.2	2	11.1	18	10	25.0	29	72.5	1	2.5	40	58	5.7
	standard	19	11.4	126	75.4	22	13.2	167	43	10.8	317	79.2	40	10.0	400	567	55.8
	light	1	3.0	21	63.6	11	33.3	33	4	4.2	55	57.9	36	37.9	95	128	12.6
Light	dark	0	0.0	4	66.7	2	33.3	6	0	0.0	11	91.7	1	8.3	12	18	1.8
	standard	3	7.0	34	79.1	6	13.9	43	0	0.0	66	79.5	17	20.5	83	126	12.4
	light	0	0.0	15	78.9	4	21.1	19	2	5.0	21	52.5	17	42.5	40	59	5.8
Total		30	9.9	227	74.7	47	15.5	304	74	10.4	521	73.2	117	16.4	712	1016	100.0

Table 3. Blue dun shade distribution in progeny of sires or dams of a given shade

Parent		Progeny							
		stallions				mares			
		dark	standard	light	Total	dark	standard	light	Total
Dark sires	N	4	14	0	18	15	22	5	42
	%	22.2	77.8	0.0	100	35.7	52.1	11.9	100
Dark dams	N	5	17	4	26	13	41	2	56
	%	19.2	65.4	15.4	100	23.3	73.2	3.6	100
Standard sires	N	23	160	35	218	57	401	77	535
	%	10.5	73.4	16.1	100	10.7	75.0	14.4	100
Standard dams	N	24	174	28	226	54	398	61	513
	%	10.6	77.0	12.4	100	10.5	77.6	11.9	100
Light sires	N	3	53	12	68	2	98	35	135
	%	4.4	77.9	17.6	100	1.5	72.6	25.9	100
Light dams	N	1	36	15	52	7	82	54	143
	%	1.9	69.2	28.8	100	4.9	57.3	37.8	100

Phenotypic quantitative distributions in stallions and mares resulted from more numerous standard horse *inter se* matings, as well as from all of the matings are alike ($p>0.05$; Table 2). This fact indicates that the shade inheritance may be sex-limited only to a little extent. Thus, the present results do not confirm the model based on different phenotypic segregation ratios in stallions and mares, suggested in former studies [9]. They were conducted on several times fewer horses and this could be the cause of the inconsistency.

The phenotypic segregation ratio in progeny produced by *inter se* standard horse matings: 10.9% dark shaded horses, 78.1% standard shaded horses and 10.9% light shaded horses (Table 1) may suggest that the shades are controlled by three pairs of autosomal alleles which act similarly. However, in such case this phenotypic distribution should agree with that in the whole progeny, which is not observed. The model in question is also shaken by almost 75% standard shaded horses in the population which remain constantly in spite of no selection for the shade and no preference for any special kinds of matings with regard to the shade. Moreover, it is in disagreement with the segregation ratio in the progeny of both light parents: too numerous standard foals compared with too few light foals.

The results do not indicate the shades might be controlled by allele series from one locus, either.

Hence, it should be analysed if the shades may be governed by *E* and *D* loci, which are responsible for the blue dun coat colour. Relatively low dark and light shade frequency, high standard shade frequency, as well as the known *E* allele activity causing the intensive black melanogenesis [8] and that of *D* allele which involves the pigment decrease, lead to consider the following model of inheritance:
EEDd – dark shaded horses;
EEDD and *EeDd* – standard shaded horses;
EeDD – light shaded horses.

Since e.g. *EeDd* horses are standard and not dark, whereas a black horse may be both *EEdd* and *Eedd*, not equal activity of both loci is assumed in the model. *E* allele would darken the colour more intensively than *D* allele could lighten it (or vice versa: *e* allele would lighten the colour less efficaciously than *d* allele could darken it). Regarding the frequency of recessive *e* (0.1536) and *d* (0.1024) alleles in the population of 514 Polish Konik horses in 2002 [11], the expected frequency of dark, standard and light phenotypes, according to the suggested model, amounts to 0.136, 0.657 and 0.217, respectively. The frequencies observed in the present study are slightly different since there are more standard shaded horses. However, it should be pointed out that in both cases the segregation ratio asymmetry, which has been shown, is similar: the actual proportion of light horses to dark horses amounted to 1.58 and the expected one to 1.59.

Foal genotypes, which may be produced by all examined matings, according to the proposed model, are presented in Table 4. Most matings resulted in phenotypes consistent with the expectation. Only light shaded parents should not have produced dark foals. It would not be possible that a black horse crossed with a standard and with a light one foaled two light descendants, either. However, checking the material reveals that one of the horses recorded in the Studbook as dark by both light parents, *3823 Nowina* mare, was standard in fact. The cases of inconsistency may often result from the difficulty in the proper phenotype identification. In the nature, the coat colour shade seems to be a continuous character. Lots of horses are of an intermediate shade, which is difficult to classify. Moreover, as it has been mentioned in the Introduction, the hair colour is influenced by some environmental factors. The coat hair in horses of various blue dun shades differs particularly in white light remission [10]. The moderate heritability of the character (h^2=0,398) probably confirms that the environmental factors somewhat disturb the proper phenotype identification.

Table 4. Genotypes expected according to the suggested inheritance model and observed progeny number produced in various matings

Parents	Progeny						
	n	dark	standard	light	black	red dun	chestnut
Dark x dark *EEDd x EEDd*	7	*EEDd* 5	*EEDD* 1	- 0	*Eedd* 1	- 0	- 0
Dark x standard *EEDd x EEDD, EeDd*	106	*EEDd* 26	*EEDD* *EeDd* 71	*EeDD* 7	*EEdd* *Eedd* 2	- 0	- 0
Dark x light *EEDd x EeDD*	26	*EEDd* 1	*EEDD* 21	*EeDD* 4	- 0	- 0	- 0
Standard x standard *EEDD, EeDd x EEDD, EeDd*	570	*EEDd* 62	*EEDD* *EeDd* 443	*EeDD* 62	*EEdd* *Eedd* 1	*eeDD* *eedd* *eeDd* 2	
Standard x light *EEDD, EeDd x EeDD*	255	*EEDd* 8	*EEDD* *EeDd* 176	*EeDD* 70	- 0	*eeDD* *eeDd* 1	- 0
Light x light *EeDD x EeDD*	59	- **2**	*EEDD* 36	*EeDD* 21	- 0	*eeDD* 0	- 0
Dark x black *EEDd x EEdd, Eedd*	2	*EEDd* 2	*EeDd* 0	- 0	*EEdd* *Eedd* 0	- 0	- 0
Standard x black *EEDD, EeDd x EEdd, Eedd*	19	*EEDd* 5	*EeDd* 11	- **1**	*EEdd* *Eedd* 0	*eeDd eedd* 2	
Light x black *EeDD x EEdd, Eedd*	4	*EEDd* 1	*EeDd* 2	- **1**	- 0	*eeDd* 0	- 0
Dark x red dun/chestnut *EEDd x eeDD, eeDd, eedd*	1	- 0	*EeDd* 1	*EeDD* 0	*Eedd* 0	- 0	- 0
Standard x red dun/chestnut *EEDD, EeDd x eeDD, eeDd, eedd*	16	- 0	*EeDd* 14	*EeDD* 2	*Eedd* 0	*eeDD* *eeDd* 0	*eedd* 0
Light x red dun/chestnut *EeDD x eeDD, eeDd, eedd*	1	- 0	*EeDd* 1	*EeDD* 0	- 0	*eeDD* *eeDd* 0	- 0
Total	1066	112	777	168	4	5	

Progeny number of a genotype not consistent with the model is marked with (bold).

In turn, black *Gazda 1/Ol* sired both light shaded foals. It is known, the fact, how difficult sometimes it is to define if a horse is dark blue dun or black. Some people even classify it as a “black-blue-dun”. Maybe the sire still carried *D* gene. It seems that single horses of colours or shades not consistent with the model, can result from a mistake, not proper colour definition or even parentage inconsistency and they should not exclude the rule.

As a matter of fact, it is not possible to analyse the phenotypic distributions regarding the non-blue-dun horses, since, as it has been stated, almost all such individuals have been eliminated from the breeding. Taking into account only blue dun horses, it can be noticed that as a result of most of the matings, relatively too numerous standard foals appear. It can be a consequence of the difficulties in proper phenotype recognition. The observed recessive allele frequencies in the population, as well as more common use of some carriers of these alleles in some kinds of matings, certainly play the decisive role. The asymmetry in phenotypic distribution is the most significant and is possible to explain with the suggested mode of inheritance.

Further studies are necessary for the final solution of the blue dun shade inheritance. Maybe another, hitherto not known gene participates in the mechanism. It is interesting, the fact, that the segregation ratios in the progeny of the horses registered in the first five volumes of the Studbook show similar tendencies as in the whole population.

CONCLUSIONS

1. On the basis of phenotypic segregation ratio in the progeny of variously shaded blue dun parents it can be stated, that the shades mainly depend on the horse genotype, though the environmental factors also play a certain role.
2. The blue dun shade character can be controlled by the known alleles from *E* and *D* loci, which govern the blue dun coat colour appearance.

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