



ORIGINAL ARTICLE

Estimation of genetic parameters for hip dysplasia in Czech Labrador Retrievers

L. Vostrý^{1,2}, Z. Čapková¹, N. Šebková¹ & J. Přibyl^{1,2}

¹ Faculty of Agrobiological, Food and Nature Resources, Czech University of Life Science Prague, Prague, Czech Republic

² Institute of Animal Science, Prague-Uhřetěves, Czech Republic

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Correspondence

Luboš Vostrý, Faculty of Agrobiological, Food and Nature Resources, Czech University of Life Science, Kamýcká 129, 165 21 Prague 6-Suchbát, Czech Republic. Tel: +420 22438 2547; Fax: +420 234 381 801; E-mail: vostry@af.czu.cz

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Summary

The objective of this study was to estimate the genetic parameters, genetic trends and breeding values using linear model (LM) and threshold model (TM) for the development of hip dysplasia (HD) in Labrador Retrievers in the Czech Republic ($n = 3151$). The right and left hip joints were evaluated separately using the Fédération Cynologique Internationale scoring system. Four linear and four TMs were tested for the correct estimation of genetic parameters. All the tested models utilized fixed effects of sex, assessor, year of birth, regression of age at evaluation, random direct genetic effects and the effect of the animals' permanent environments. The models differed in the inclusion of the following effects: fixed effects of regression of inbreeding coefficient, random maternal effect and random effect of the maternal permanent environment. Compared to the TM, the LM provided lower coefficients of direct (0.25–0.29 versus 0.26–0.35) and maternal heritability (0.01–0.02 versus 0.03–0.05), repeatability (0.76–0.77 versus 0.78–0.83) and of the correlation between direct and maternal effects (–0.55 to –0.21 versus –0.80 to –0.27). In the tested models, no statistical significance was found for fixed regression of inbreeding coefficients or for the random effect of the permanent maternal environment. In spite of the similarity of the LM and TM results, the TM is recommended as the more suitable model for estimating genetic parameters and subsequent breeding values for HD in Labrador Retrievers in the Czech Republic.

Introduction

Hip dysplasia (HD) is a developmental hereditary disease of the hip joints. It is one of the best-known and most widespread diseases in dogs, and it has significant economic and breeding impacts. Hip dysplasia is an orthopaedic problem affecting mainly large and giant dogs breeds (Ginja *et al.* 2009) and fast-growing dogs such as the Labrador Retriever, and its

severity may be influenced by many environmental factors (Silvestre *et al.* 2007). In many studies, HD is considered to be a quantitatively conditioned trait influenced by many minor genes and environmental factors that affect the growth rate and the physical strain of developing hip joints (Mäki *et al.* 2000; Hamann *et al.* 2003; Sturano *et al.* 2006). Heritability of HD in dogs is estimated in range from 0.20 to 0.60 (Malm *et al.* 2007).

In the Czech Republic, the five-point scale (A, B, C, D and E) Fédération Cynologique Internationale (FCI) scoring system is used. For accomplishment of breeding rules, the dogs must have X-ray of hips with A, B or C degree of HD. In the breeding programme of Labrador retriever in the Czech Republic, the animals with A or B degree of HD can be mated without limitation. Animals with C degree of HD can be mated only with dogs with A or B classifications of the HD. Dogs with D or E HD are excluded from breeding.

In this disease, disease hip joint laxity, subluxation or incorrect configuration of the femoral head and acetabulum are typical (Lust *et al.* 1993). Clinical signs can be present in animals younger than 1 year old or in adults. However, many affected dogs have minimal or no clinical signs (Ginja *et al.* 2009). Phenotypic manifestations of HD are gait abnormalities, shortened stride, pelvic limb muscle atrophy or reluctance to walk on stairs (Fry & Clark 1992). In many countries, a ventrodorsal radiograph of the pelvis is the most common method for HD detection, and potential breeding animals must be above a given minimum age, usually at the age from 12 to 24 months. For early detection of HD, many methods have been created, and most of these methods are based on passive hip laxity (PHL), which is considered a primary risk factor for HD (Smith *et al.* 1995). PHL is the basis of the Ortolani test and the PennHIP method (Lust *et al.* 1993; Smith *et al.* 1995). In both the methods, the distraction index and the Norberg angle can be measured and evaluated for puppies as young as the age of 4 months (Lust *et al.* 1993). Other methods for early detection of HD are palpation and range of motion tests (Ginja *et al.* 2010). The first signs of HD, femoral head subluxation and development of an acetabular rim, can also be detected through radiographic techniques (Riser 1975). A radiographic examination of the coxofemoral joint has been included in breeding programmes in many breeders clubs with the aim of reducing the incidence of the disease (Sturano *et al.* 2006). Veterinarians have adopted various methods for treatment of clinical HD-affected dogs, such as triple pelvic osteotomy, femoral head and neck excision or pubic symphysiodesis (Bernardé 2010).

In the majority of dog breeding programmes, selection is mostly based on the phenotypic expression of animals, and variable results are obtained (Leppänen *et al.* 2000). Lower efficiency of selection of HD is obtained with mere phenotypes compared

to traits with high heritability (Zhu *et al.* 2009). For this reason, the selection of parents should be based on the individual genetic value of an animal (the so-called breeding value) as estimated by mixed linear models (LMs) using the animal model method BLUP.

The estimation of genetic parameters and subsequently of breeding value for HD has been studied by many authors using various methods and a variety of dog breeds (Leppänen *et al.* 2000; Mäki *et al.* 2000; Hamann *et al.* 2003; Sturano *et al.* 2006; Silvestre *et al.* 2007; Engler *et al.* 2008 and Malm *et al.* 2008). Malm *et al.* (2008) also investigated the genetic variation of HD in Rottweilers, as well as the suitability of transforming categorical HD variables into linear variables. Silvestre *et al.* (2007) compared the suitability of threshold models (TMs) to that of LMs in estimating genetic parameters of HD.

The objective of this paper was to estimate genetic parameters and genetic trends for HD. Another objective was to compare the components of variance and genetic parameters between a LM and a TM and find a suitable model for the genetic analysis for HD.

Material and methods

Data

Data and pedigree information for the analysis of HD incidence in Labrador Retrievers in the Czech Republic were provided by the Club of Hunting Tracker Breeders. The data contained the official evaluation of HD according to the FCI scoring system for 3151 dogs over the course of 16 years (1991–2007). The right and left hip joints were evaluated separately. Every evaluated animal had two measurements on both sides. The grade of HD was evaluated by eight veterinarians. The evaluation was made on both sexes. The data also contained information on the date of birth, age, sex and assessor's identification number. Dogs were scored in five categories from A to E according to the FCI scoring system; for the data analysis, the original scores were coded as numbers from 0 to 4.

Statistical model

Significant differences between left and right hip joints were evaluated using paired sample Wilcoxon rank sum test (SAS, 2005) and differences between

inbreeding coefficients for male and female dogs were evaluated using the *t* test. The influence of different parameters on HD incidence was preliminarily evaluated using a LM with fixed effects using the GLM procedure of the SAS (2005):

$$y_{ijkl} = \mu + \text{Sex}_i + \text{Asse}_j + \text{YearB}_k + \text{Sire}_l + b_1 \cdot \text{Age} + b_2 \cdot \text{Fx} + e_{ijkl}, \quad (1)$$

where y_{ijkl} – HD evaluation (3151 measurements), μ – general mean, Sex_i – fixed effect of *i*th sex (*i* = male, female), Asse_j – fixed effect of *j*th assessor (*j* = 1, ..., 8), YearB_k – fixed effect of *k*th year of birth (*k* = 1, ..., 17), Sire_l – fixed effect of *l*th sire (*l* = 1, ..., 124), $b_{1,2}$ – fixed regression coefficients, Age – effect of age at evaluation, Fx – effect of inbreeding coefficient and e_{ijkl} – residual error.

Although live weight is also a significant effect influencing HD incidence, it was not included in the analysis because live weight was not accessible.

This model was used for the definition of statistical significance of the fixed effect only for further analysis. Therefore, these models do not use relationships between sires, and no genetic variance was assumed.

Inbreeding coefficient

Complete pedigree information with more than eight generations of ancestors covering the dogs with HD evaluations was used to estimate the inbreeding coefficient (*F_x*). The INBREED procedure of the SAS (2005) was employed for *F_x* estimation. The coefficient (*F_x*) was estimated as a coancestry coefficient (Falconer & Mackay 1996).

$$F_X = f_{ZY} = 0.25 (f_{AC} + f_{AD} + f_{BC} + f_{BD}), \quad (2)$$

where *f* is the coancestry coefficient between two individuals, e.g. for X and Y, A and B are the parents of individual X, and C and D are the parents of individual Y.

The completeness of the pedigree information (up to eight generations of ancestors), which is of great importance for estimating the *F_x*, was evaluated by (Cassell *et al.* 2003):

$$cp = \frac{a_k}{\sum_{i=1}^g 2^i}, \quad (3)$$

where *cp* – the coefficient of pedigree completeness, and a_k – the number of known ancestors in *g* generations.

Table 1 Tested models according to tested random effects

Models	<i>a</i>	<i>m</i>	pe	me
I	x		x	
II	x	x	x	
III	x	x	x	x
IV	x		x	x

a – additive direct genetic effect, *m* – additive maternal genetic effect, pe – effect of animal permanent environment and me – effect of permanent maternal environment.

Estimation of genetic and environmental parameters

With regard to fixed effects selected according to the above-mentioned model, components of variance in the genetic parameters were estimated by a LM and a TM. Different models were tested in this work to determine a more suitable model for the estimation of genetic and environmental parameters. Both models included the following fixed effects: sex, assessor, linear regression of age at the HD evaluation, year of birth and linear regression of coefficient of inbreeding. The tested models in consideration of random effects are shown in Table 1.

It is assumed that the direct and maternal effects are correlated and that the remaining effects (animal permanent environment, permanent maternal environment and residual errors) are independent of each other. Furthermore, it is assumed that the effects show a normal random distribution with a mean of zero and variance:

$$\begin{aligned} V \begin{bmatrix} a \\ m \end{bmatrix} &= A \begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix} \\ V(\text{pe}) &= I\sigma_{\text{pe}}^2, \\ V(\text{me}) &= I\sigma_{\text{me}}^2, \\ V(e) &= I\sigma_e^2 \end{aligned} \quad (4)$$

where σ_a^2 – additive genetic variance of direct effect, σ_m^2 – additive genetic variance of maternal effect, σ_{am} – genetic covariance of direct and maternal effect [Cov(*a, m*)], σ_{pe}^2 – variance of the effect of animal permanent environment, σ_{me}^2 – variance of the effect of permanent maternal environment, σ_e^2 – variance of the effect of residual error, *A* – relationship matrix and *I* – identity matrix.

The following population parameters were derived from the estimated variance–covariance components (Willham, 1972):

$$\begin{aligned}
\sigma_{\text{gt}}^2 & - \text{total additive genetic variance} \\
& [\sigma_{\text{gt}}^2 = \sigma_a^2 + 1.5\sigma_{\text{am}} + 0.56\sigma_m^2] \\
\sigma_y^2 & - \text{phenotype variance} \\
& [\sigma_y^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{\text{am}}^2 + \sigma_{\text{me}}^2 + \sigma_{\text{pe}}^2 + \sigma_e^2] \\
h_a^2 & - \text{coefficients of direct heritability} \\
& [h_a^2 = \sigma_a^2 / \sigma_y^2] \\
h_m^2 & - \text{coefficients of maternal heritability} \\
& [h_m^2 = \sigma_m^2 / \sigma_y^2] \\
h_t^2 & - \text{total heritability } [h_t^2 = \sigma_{\text{gt}}^2 / \sigma_y^2] \\
c_a^2 & - \text{the ratio of animal permanent environment} \\
& \text{variance to phenotype variance } [c_a^2 = \sigma_{\text{pe}}^2 / \sigma_y^2] \\
c_m^2 & - \text{the ratio of maternal permanent environment} \\
& \text{variance to phenotype variance } [c_m^2 = \sigma_{\text{me}}^2 / \sigma_y^2] \\
R & - \text{direct repeatability } [R = (\sigma_y^2 - \sigma_e^2) / \sigma_y^2]
\end{aligned} \tag{5}$$

The pedigree set for the estimation of genetic parameters comprised eight generations of ancestors ($n = 4962$ animals).

The suitability of the tested models (linear and threshold) for the estimation of genetic parameters was tested on the basis of estimated values of residual variance (σ_e^2).

The various LMs were compared on the basis of Akaike's information criterion (AIC; Bozdogan 2000):

$$\text{AIC} = -2\log L(\theta) + 2d, \tag{6}$$

where $\log L(\theta)$ is the logarithm of the value of the likelihood function, and d is the number of free parameters in the model.

The various TMs were compared on the basis of the deviance information criterion (DIC, Spiegelhalter *et al.* 2002):

$$\text{DIC} = \bar{D}(\theta) + p_D, \tag{7}$$

where $\bar{D}(\theta)$ is the posterior expectation of the Bayesian deviance representing a measure of the fit of the model, and p_D is the effective number of parameters representing penalty for increasing model complexity.

For the estimation of variance and covariance components, the REMLF90 program (Misztal *et al.* 2002) was used for the LM and the THRGIBBS1F90 program (Misztal *et al.* 2002), which applies the Bayesian approach by means of the Gibbs sampling algorithm, was used for the TM. According to a graphical representation, the first 3000 samples were excluded as the burn-in. A total of 30 000 samples were used to estimate the posterior mean and SD of the variance components.

Breeding values (BV) were estimated using the BLUPF90 and CBLUP90THR computer programmes (Misztal *et al.*, 2002). The Spearman's rank correlation coefficient (r_S) and Pearson correlation coefficient (r_P) were used to compare the breeding value estimated by LM and TM in two data subsets – Data 1 – the set of all dogs including those with pedigree data ($n = 4962$) and Data 2 – the subset of observed dogs ($n = 3151$).

Results and discussion

Both hip joints received a score of 0 in the majority of cases (approximately 40%) (Table 2). The incidence in more severe classes of HD decreased gradually. The most severe score was given to approximately 5% of the examined dogs. The comparison of the right and left hip joints indicated that the left hip joint was afflicted by worse grade HD. Possible explanation is laterality of dogs. This difference between left and right joints was found to be statistically significant ($p < 0.01$).

The number of offspring from 124 sires ranged from 10 to 183 [mean 73, standard deviation (SD) 62], and the number of offspring from 773 dams ranged from 2 to 64 (mean 10, SD 5) (Table 3). The age of the evaluated animals ranged from 9 to 35 months (mean 17.8, SD 2.6). Most of the dogs (approximately 77%) were evaluated between 15 and 22 months of age.

Analysis of fixed effects

The fixed effects included in the model were statistically significant at the 0.1‰ (assessor, sire, year of birth and fixed regression coefficients on age) or the 1‰ level (sex). Statistically non-significant effect was only inbreeding depression ($p = 0.641$).

Small differences between male and female dogs were found, with female dogs having lower HD. This

Table 2 Distribution of HD score incidence for the right and left hip joints in 3151 dogs

Categories	Left hip joint	Right hip joint
	No. of hips (%)	No. of hips (%)
0	1241 (39)	1321 (42)
1	722 (23)	696 (22)
2	659 (21)	669 (21)
3	344 (11)	303 (10)
4	179 (6)	156 (5)

HD, hip dysplasia.

Table 3 Pedigree structure of animals with measurements ($n = 3151$) according to sex

Sires ($n = 124$)		Dams ($n = 773$)	
Number of offsprings	Number (%)	Number of offsprings	Number (%)
≤ 10	13 (10)	≤ 2	209 (27)
11–30	55 (44)	3–20	372 (48)
31–60	21 (17)	11–20	149 (19)
61–90	18 (15)	21–30	28 (4)
> 90	17 (14)	> 30	15 (2)

difference may be caused by the effect of different hormones that influence, among other things, skeletal development and consequently body weight. A similar effect of sex on HD incidence was published by Wood *et al.* (2002). In contrast, Sturaro *et al.* (2006) and Dietschi *et al.* (2003) reported a higher incidence of HD in female dogs of the German Shepherd and Rottweiler breeds. Mäki *et al.* (2000) stated that HD incidence was not influenced by sex.

Age was also found to be a significant factor for HD (FCI score). Younger dogs received lower scores than older dogs. This trend corresponds to the biological principle of HD because HD is manifested at older ages. Similar conclusions were drawn by other authors (Mäki *et al.* 2000 and Sturano *et al.* 2006) in studies of other breeds.

Significant differences in FCI score were also observed between different years of birth. Compared to the other years, dogs born in 1993 received the lowest scores. The highest values were observed in dogs born in 2001 (Table 4). Differences between the years may be because of nutrition, genetic trend, the dog's physical strain, veterinary practices or by a change in environmental factors that may influence HD development in dogs. Distl *et al.* (1991), Mäki *et al.* (2000) and Malm *et al.* (2008) also found a statistically significant effect of birth year on HD incidence.

The assessor had an effect on the HP score. Mäki *et al.* (2000), Hamann *et al.* (2003) and Sturano *et al.* (2006) also reported that the assessor was a significant environmental factor.

Inbreeding coefficient

For all individuals tested, full pedigrees were traced up to generation 8 ($cp = 1$). The average value of Fx (SD) was estimated to be 0.026 (0.038) (Table 5). This value indicates a low level of inbreeding. Female dogs had a slightly higher ($p < 0.05$). In contrast, male dogs displayed higher Fx variability expressed as CV% or a larger range.

The highest average values of Fx were observed in the birth years 1991 and 1993, while the lowest values were observed in 2004 and 2006 (Figure 1). There is a downward trend of the average value of Fx from the year 1996 to 2004 (from 0.057 to 0.007). In the last evaluated years of birth (2004, 2005, 2006 and 2007), the average value of Fx varied around 0.01. However, Calboli *et al.* (2008) reported an increase in the inbreeding coefficient of Labrador Retrievers kept in the United Kingdom. However, these authors found identical values of Fx in this breed, in the range of 0–0.05. Mäki *et al.* (2001) also reported an identical range of Fx in Finnish Labrador Retrievers. These authors observed a downward trend of the average value of Fx in birth years since 1981. For the population in the present study, the general decrease in Fx values was caused by the continuous importation of unrelated animals from abroad.

In this work, no significant effects of inbreeding level on HD were detected. However, this considerable influence may be caused just by the low value of the coefficient Fx in the population of Czech Labrador Retrievers. In contrast, Engler *et al.* (2008) demonstrated an influence of inbreeding coefficient on the grade of HD.

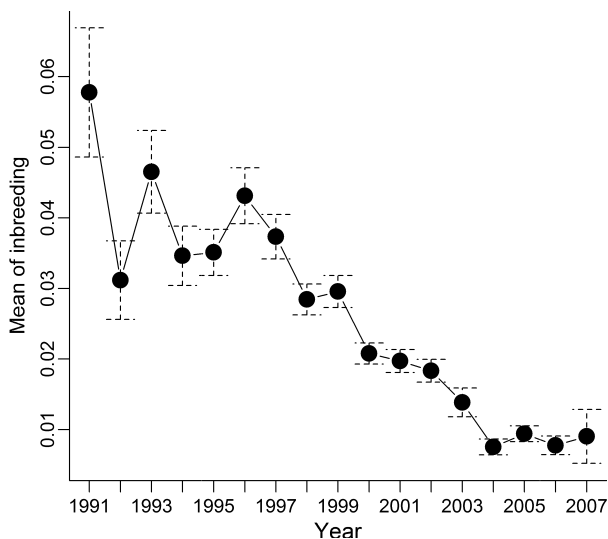
Table 4 Effect of the year of birth expressed as a deviation from the year 1991 LSMEANS = 0.69 (FCI score)

	Year of birth															
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
n	48	105	144	183	165	235	326	315	334	300	278	204	191	157	105	19
Dev.	0.07	−0.04	0.43	0.27	0.50	0.71	0.97	1.00	1.03	1.19	1.08	0.88	0.56	0.67	0.55	0.47
SE	0.20	0.19	0.21	0.20	0.21	0.21	0.21	0.22	0.21	0.20	0.22	0.23	0.23	0.24	0.24	0.29
Sig.	n.s.	n.s.	*	n.s.	*	***	***	***	***	***	***	***	*	**	*	n.s.

n – number of dogs in the given year, Dev. – deviation from the year 1991, SE – standard error of the deviation, sig. – significance level, n.s. – not significant, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$, FCI, Fédération Cynologique Internationale.

Table 5 Descriptive statistics of inbreeding coefficients for the evaluated dogs

	All	Males	Females
Mean	0.026	0.023	0.027
SE	0.001	0.001	0.001
Min.	0.000	0.000	0.000
Max	0.313	0.313	0.289
CV%	1.526	1.617	1.465

**Figure 1** Development of the average value of inbreeding coefficient by the years of birth (with SE)

Genetic parameters

Linear model

The highest value for the variance component because of direct effect (σ_a^2) was estimated by Model I ($\sigma_a^2 = 0.391$), while the lowest value was estimated by Model IV ($\sigma_a^2 = 0.327$) as shown in (Table 6). In the variance component because of maternal effect (σ_m^2), Model II provided the highest value ($\sigma_m^2 = 0.025$), and Model III provided the lowest value ($\sigma_m^2 = 0.013$). The inclusion of maternal effect in the model caused a reduction in σ_a^2 . In Models III and IV, which included the random effect of the permanent maternal environment (me), a further decrease in σ_a^2 was observed, as well as a marked decrease in the value of σ_m^2 (by approximately 50%) in Model III. The values of σ_{gt}^2 estimated for the particular models were in the range of 0.318–0.391. The highest values of σ_{gt}^2 were estimated by Model I, which did not include maternal effect, so they corresponded to the value of σ_a^2 . The lowest values of σ_{gt}^2 were estimated by Model III, which included both

maternal effect and the effect of the permanent maternal environment.

The residual variance (σ_e^2) did not change between the models ($\sigma_e^2 = 0.323$). In contrast, the AIC values did change between the models (Table 6). The highest values of AIC were found in Models I and IV. The lower values of AIC in Models II and III indicated the greater suitability of these models compared to Model I. However, the identical estimated values of AIC between Models II and III indicate the greater suitability of the simpler Model II compared to the more complicated Model III, and it is advisable to use a simpler model if the AIC values are identical.

Similar to the variances of the genetic components, the direct heritability coefficients were similar among the LMs. The highest value of the coefficient of direct heritability (h_a^2) was estimated by LM I, and the lowest was estimated by Model IV. Similarly to h_a^2 , the coefficient of maternal heritability (h_m^2) paralleled the fluctuations in σ_a^2 and σ_m^2 in the LMs. These estimates of σ_a^2 are in the range published by other authors (Wood *et al.* 2002; Dietschi *et al.* 2003; Sturano *et al.* 2006 and Malm *et al.* 2008), who estimated h_a^2 to be in the range of 0.15–0.42, and others (Dietschi *et al.* 2003; Hamann *et al.* 2003 and Sturano *et al.* 2006), who estimated h_m^2 in the range of 0.02–0.11. This wide range in estimations is influenced by the use of different methods of heritability coefficient estimation (such as parent–offspring regression and the REML animal model), by the inclusion of different effects in the models and by differences in breeds, environmental conditions and breeding aim. The values of h_t^2 were estimated to range from 0.237 to 0.288.

The genetic correlation between direct and maternal effects was within the range of –0.213 to –0.546 in the tested LMs. The effect of the permanent maternal environment had the highest influence on the value of r_{am} , wherein the inclusion of this effect led to a twofold decrease in the value of r_{am} . Hamann *et al.* (2003) estimated the values of r_{am} to range from –0.522 to 0.621.

The highest significance in models was found for the effect of the animal permanent environment, which accounted for approximately 47–52% of total phenotype variability (Table 6). The repeatability coefficient (R) in the LMs did not change markedly between the tested models, similar to the other coefficients. The value of R ranged from 0.751 (Model IV) to 0.762 (Model I). Although the value of R was similar, the inclusion of maternal effects in the model slightly decreased this value. This slight

	I	II	III	IV
AIC	16 755	9230	9230	16 589
σ_a^2	0.391 (0.043)	0.379 (0.057)	0.368 (0.057)	0.327 (0.081)
σ_m^2		0.025 (0.016)	0.013 (0.015)	
σ_{am}		−0.021 (0.024)	−0.038 (0.025)	
σ_{gt}^2	0.391	0.360	0.318	0.327
σ_{me}^2			0.030 (0.035)	0.000 (0.000)
σ_{pe}^2	0.643 (0.030)	0.644 (0.034)	0.641 (0.014)	0.670 (0.047)
σ_e^2	0.323 (0.006)	0.323 (0.006)	0.323 (0.006)	0.323 (0.006)
σ_y^2	1.357	1.350	1.337	1.295
h_a^2	0.288	0.281	0.275	0.252
h_m^2		0.018	0.010	
h_t^2	0.288	0.267	0.237	0.252
c_a^2	0.474	0.477	0.480	0.517
c_m^2			0.022	0.000
R	0.762	0.761	0.758	0.751
r_{am}		−0.213	−0.546	

Table 6 Genetic parameter estimation by the linear models

AIC – Akaike's information criterion, σ_a^2 – additive genetic variance of direct effect, σ_m^2 – additive genetic variance of maternal effect, σ_{am} – genetic covariance of direct and maternal effect [Cov(a,m)], σ_{me}^2 – variance of the effect of permanent maternal environment, σ_{pe}^2 – variance of the effect of animal permanent environment, σ_e^2 – variance of the effect of residual error, σ_y^2 – phenotype variance, h_a^2 – coefficients of direct heritability, h_m^2 – coefficients of maternal heritability, h_t^2 – total heritability, c_a^2 – the ratio of animal permanent environment variance to phenotype variance, c_m^2 – the ratio of maternal permanent environment variance to phenotype variance, R – direct repeatability.

decrease is caused by the reduction in σ_a^2 by the above-mentioned σ_m^2 . The other effects had less influence on the value of R . High values of R showed similar levels of development of HD for both hip joints. Similar conclusions were drawn by Wood *et al.* (2002), who reported a high coefficient of correlation between the grade of HD development in the left and right hip joints in Labrador Retrievers. These authors also stated that the coefficient of regression between the grades of HD development in both hip joints was close to 1 ($b \approx 1$). Silvestre *et al.* (2007) published a higher value of HD incidence repeatability in a LM for the Estrela mountain dog ($R = 0.83$).

The effect of the permanent maternal environment accounted for approximately 2% of the total variability. Dietschi *et al.* (2003) reported that the effect of the permanent maternal environment accounted for 10% of the total variance. The value published in this paper is at the lower boundary of the interval estimated for the effect of litter published by Mäki *et al.* (2000). The effect of litter, used in these cited work, can be used as approximation of the effect of the permanent maternal environment. Dietschi *et al.* (2003) suggested that the maternal environment effect can be strongly confounded with the effect of litter.

Threshold model

The values of σ_a^2 in the TMs (Table 7) were estimated to range from 0.293 to 0.387. The highest value of σ_a^2 was estimated by Model III. The inclusion of maternal effects in the models brought about a minute decrease in the value of σ_a^2 between Models I and II. However, the greatest increase σ_a^2 was detected between Models IV and III. For maternal genetic effects, the values estimated by the TMs were in the range of 0.038–0.054. A comparison of the values of standard errors with the maternal genetic effects shows that the estimations of coefficients σ_m^2 were not significant in the models (LMs and TMs). Dietschi *et al.* (2003) reported that the maternal genetic effect was not significant if the maternal environmental effect was included. The values of σ_{gt}^2 were estimated to range from 0.267 to 0.367 in the different models. The lowest value of σ_{gt}^2 was estimated by Model III, while the highest value of σ_{gt}^2 was estimated by Model I.

The random effect of the permanent maternal environment (me) caused an increase in the value of σ_a^2 and a decrease in the value σ_m^2 in Model III. However, in Model IV, which included the random effect of the permanent maternal environment (me), a decrease in σ_a^2 was observed. In Model III, there

Table 7 Genetic parameter estimation by the threshold models

	I	II	III	IV
DIC	−24 386	−41 330	−32 126	−26 275
σ_a^2	0.367 (0.067)	0.363 (0.093)	0.387 (0.102)	0.293 (0.059)
σ_m^2		0.054 (0.029)	0.038 (0.020)	
σ_{am}		−0.038 (0.127)	−0.093 (0.047)	
σ_{st}^2	0.367	0.333	0.267	0.293
σ_{me}^2			0.070 (0.027)	0.058 (0.023)
σ_{pe}^2	0.601 (0.181)	0.594 (0.167)	0.530 (0.125)	0.600 (0.146)
σ_e^2	0.192 (0.052)	0.195 (0.051)	0.184 (0.038)	0.193 (0.044)
σ_y^2	1.160	1.168	1.116	1.144
h_a^2	0.316	0.311	0.347	0.256
h_m^2		0.046	0.034	
h_t^2	0.316	0.287	0.239	0.256
c_a^2	0.518	0.509	0.475	0.524
c_m^2			0.063	0.051
R	0.832	0.833	0.835	0.831
r_{am}		−0.271	−0.801	

DIC – Deviance information criterion, σ_a^2 – additive genetic variance of direct effect, σ_m^2 – additive genetic variance of maternal effect, σ_{am} – genetic covariance of direct and maternal effect [Cov(a,m)], σ_{me}^2 – variance of the effect of permanent maternal environment, σ_{pe}^2 – variance of the effect of animal permanent environment, σ_e^2 – variance of the effect of residual error, σ_y^2 – phenotype variance, h_a^2 – coefficients of direct heritability, h_m^2 – coefficients of maternal heritability, h_t^2 – total heritability, c_a^2 – the ratio of animal permanent environment variance to phenotype variance, c_m^2 – the ratio of maternal permanent environment variance to phenotype variance, R – direct repeatability.

was a further decrease in the genetic covariance between direct and maternal effects. In model III, σ_{me}^2 reached twice the value of σ_m^2 . Different values of σ_{pe}^2 were estimated in the different models. The highest value of σ_{pe}^2 was estimated by Model I (0.601), and the lowest was estimated by Model III (0.530).

The residual variances in the tested TMs ranged from 0.184 to 0.195. The lowest values of σ_e^2 were estimated by Model III. The inclusion of the random effect of the permanent maternal environment and the random genetic maternal effect led to a decrease in σ_e^2 . The lower values of σ_e^2 indicate the greater suitability of these models for estimating genetic parameters.

According to DIC, Model II was favoured compare to other models (Table 7). The DIC of Model II was two times lower than the DIC of Models I and IV and 80% lower than the DIC of Model III. This indicated that Model II is not overparameterized relative to Models I and IV. The higher values of DIC in Model III indicated that this model is overparameterized relative to Model II.

In the TMs, h_a^2 ranged from 0.256 to 0.347. The highest value of h_a^2 was estimated by Model III. The

values of h_m^2 were less variable between the tested models than h_a^2 , ranging from 0.034 to 0.046. These values are consistent with the values published in the literature (Dietschi *et al.* 2003; Hamann *et al.* 2003 and Sturano *et al.* 2006). Although h_m^2 and σ_m^2 were generally low, Model II was significant with respect to DIC. This is because dams influence their offspring during pre- and post-natal development in multiple ways, such as maternal behaviour, maternal effects on birth weight and milk production, which affect body weight. All these factors may influence the subsequent formation of hip joints. The lowest value of h_t^2 was estimated by Model I, while Model II provided the highest value of h_t^2 . No estimations of h_t^2 for HD were found in the literature.

Selection of a suitable model

Based on the results, Model II shows the greatest suitability for estimating genetic parameters, both in the LM and TM form. In the LM, this model was selected on the basis of its greater suitability for estimating genetic parameters of HD grade evaluated by means of AIC and its lower number of estimated parameters. In the TM, this model was selected by means of DIC, on the basis of its lower value of σ_e^2 and its inclusion of effects that better correspond to the biological principles of HD (maternal effects). The random effect of the permanent maternal environment explained only a minute part of the variability, and for this reason, these effects were not included in further analyses. Only Model II will be used for subsequent analyses.

As shown in Tables 6 and 7 and in Figure 2, higher values of genetic parameters were obtained in the TMs than in the LMs. The highest changes between the LMs and TMs were found for σ_e^2 . These results are in agreement with the conclusions published by Silvestre *et al.* (2007).

Genetic trends and breeding value

Owing to the difference in scales in the linear and TMs, breeding values were standardized by the genetic standard deviation. The graphs (Figure 2) document an improvement in HD incidence since 1993 that is expressed by BV. In 2007, a slight decrease in the levels in 2002–2004 was observed. The improvement in HD incidence was caused by the introduction of parent pair selection on the basis of HD phenotype values. Falconer & Mackay (1996) reported that selection on the basis of phenotype for

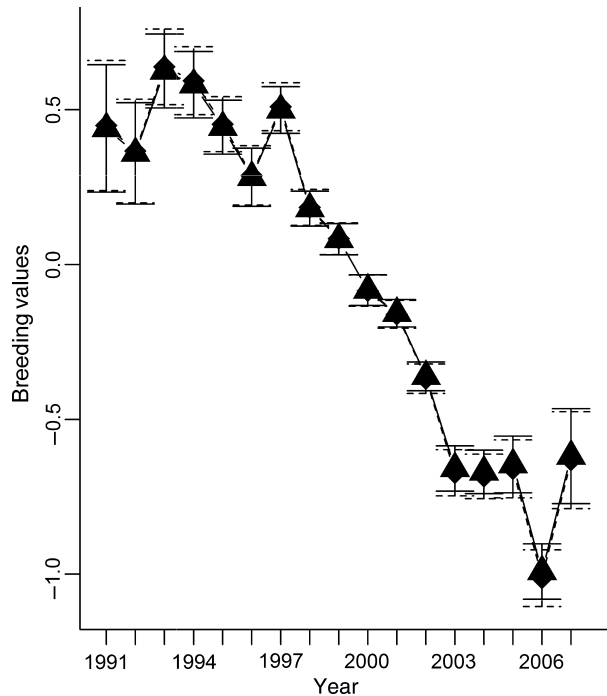


Figure 2 Genetic trend of hip dysplasia in dogs born between 1991 and 2007 estimated by the linear model (triangle) and the threshold model (square).

categorical traits is less efficient than for continuous traits. Leppänen *et al.* (2000) also reported low genetic improvement in the Finnish population of German Shepherds as a result of phenotypic selection.

Data 2 showed a closer relation between the breeding values estimated by the LM and the TM than did Data 1 (r_P and r_S ranged from 0.94 to 0.98). The greater changes in breeding value and dog rank in Data 1 are because of the fact that unclassified dogs were included in this set, and BV was estimated only on the basis of pedigree value. In these dogs, the accuracy of the BV estimate is low, so there may be changes between the models. Silvestre *et al.* (2007) estimated lower values of r_S . This difference may be caused by the higher number of dogs included in this analysis. Similar correlation coefficients between TMs and LMs were estimated for other threshold traits and species, e.g., mastitis (0.99) (Heringstad *et al.* 2003). In some papers, the suitability of a TM was compared with that of a LM both with simulated data (Abdel-Azim & Berger 1999) and real data (Silvestre *et al.* 2007). The authors reported that TMs were more suitable than LMs for categorical data. Abdel-Azim & Berger (1999) also stated that comparable values between

LMs and TMs were obtained only when the categorical traits involved more categories (approximately 10), which allows approximation of normal distribution of the categorical data. These authors further concluded that with categorical data with a small number of classes that are skewed from a normal distribution, it is more advantageous to use a TM instead of data transformation or a new variable with an LM. Contrary, Matos *et al.* (1997) did not find any differences between LMs and TMs when categorical data were evaluated.

Conclusion

The Model II with fixed effects of sex, assessor, year of birth, regression of age at evaluation, random direct, maternal effect and animal permanent environment was the most suitable of the tested models for estimating genetic parameters of HD development, on the basis of the information criteria (AIC or DIC), residual error and the ratio of the component of variance in both models (LM and TM). The fixed effect of inbreeding coefficient and the random effect of the permanent maternal environment were not statistically significant.

The results also indicate that both LM and TM can be used to estimate genetic parameters and HD breeding value of Labrador Retrievers in the Czech Republic. However, higher heritability and repeatability were obtained with the TMs. We recommend using TMs to estimate genetic parameters and determine breeding values for HD.

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