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Analysis of systematic and genetic effects on weight and body measurements and their relationships with canine hip dysplasia in German shepherd dogs

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Dedicated to my husband and my family

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Table of abbreviations

Abb.	Abbildung
b	regression coefficient
BLUP	Best Linear Unbiased Prediction
BMI	body mass index
BV	breeding value
BW	body weight
bzw.	beziehungsweise
ca.	circa
CC	chest circumference
CH	chest height
CHD	canine hip dysplasia
cm	Zentimeter
COV_a	additive genetic covariance
COV_{am}	covariance between additive genetic variance of the animal and additive genetic maternal variance
D	dam
Diss.	Dissertation
DSH	Deutscher Schäferhund
e	residual effect, comprising all effects not explained by the other effects in the model
ED	elbow dysplasia
et al.	et alii
evtl.	eventuell
F	F-Wert
FCI	Fédération Cynologique Internationale
Fig.	Figure
FG	Freiheitsgrade
g	Gramm
GS	Gibbs sampling
GSD	German shepherd dog
h^2	heritability, Heritabilität

h_a^2	heritability of the animal
h_m^2	maternal heritability
HD	Hüftgelenkdysplasie
kg	Kilogramm
KG	Körpergewicht
LR	Labrador Retriever
LS	least squares
log	logarithmisch
log^2	logarithmisch-quadratisch
LSM	Least square Mittelwerte
Max	Maximum
Min	Minimum
MTGSAM	multiple trait Gibbs sampler for animal models
N/n	number
P	error probability, Überschreitungswahrscheinlichkeit
PBV	pedigree breeding value
PEDIG	prediction of inbreeding coefficients
PEST	multivariate prediction and estimation
PZW	Pedigree-Zuchtwert
QTL	quantitative trait loci
R	correlation coefficient
RBV	relative breeding value
RBV_{ind}	RBV predicted for the dog itself
RBV_{sire}	RBV predicted for the dogs sire
RBV_{dam}	RBV predicted for the dogs dam
r_g	additive genetic correlation coefficient, Additiv genetischer Korrelationskoeffizient
r_e	residual correlation coefficient
S	sire
SAS	Statistical Analysis System
SD/s.d.	standard deviation
S + D	sire and dam

SE	standard error
SV	Verein für Deutsche Schäferhunde
Tab.	Table, Tabelle
u.	und
u.a.	unter anderem
σ_a^2	additive genetic variance, Additiv genetische Varianz
σ_m^2	maternal variance
σ_p^2	phenotypic variance
σ_e^2	residual variance
vBMI	within litter variance of body mass index
VCE	variance component estimation
vgl.	vergleiche
vWH	within litter variance of withers height
WH	height at the withers, Widerristhöhe
z.B.	zum Beispiel

CHAPTER 1

Introduction

Introduction

In dog breeding, selection of mating partners is based on different criteria, such as conformation, performance, health traits and the like. To get permission for breeding the breeding standard, given by the German shepherd dog breeding association (SV) for German shepherd dogs (GSD), defined the lower and upper limits of body measures and health traits. Body measures, such as withers height (WH), chest height, chest circumference and body weight (BW) are routinely collected in the course of inspections for breeding approval. At this time, information on canine hip dysplasia (CHD) as one of the examined health traits has to be available already. Therefore lots of information on body measures and CHD scores more accumulated over time. So the aim of this study was to analyze the systematic and genetic effects on body measures on the one hand and to investigate if there is a relevant genetic relationship between WH, body mass index (BMI), i.e. the quotient of BW and squared WH, and CHD on the other hand, that could be used for selection against CHD. Data for body measures and CHD scores from a time period of more than 10 years were used for these investigations. As in other dog breeds, CHD is among the most important hereditary skeletal diseases in the GSD as it limits long term motility and working performance of affected dogs (DISTL et al. 1991). Therefore, as early as 1966, mass selection based on radiological screening for CHD has been introduced. Sires and dams were not allowed to reproduce if their CHD scores were above an agreed threshold. Since 1999 pedigree breeding values (PBV) for CHD are in use in the German GSD population for planning of future matings. A retrospective study on CHD in the GSD showed that the currently practiced selection strategies against CHD have not yet led to satisfactory improvement of the CHD status in the German population of GSD (Janutta *et al*. 2008). However, the predictive value of PBV for CHD has not yet been evaluated in the German population of GSD. Body measures have been mentioned as possible accessory traits when selecting against CHD. Nevertheless, data or the correlations between body measures and CHD are missing. Also the selection response for conformation and conformational homogeneity of litters has not yet been investigated in the GSD.

CHAPTER 2

Analyse von systematischen Umwelt- und genetischen Effekten auf Körpergewicht und Körpermaße beim Deutschen Schäferhund

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Analyse von systematischen Umwelt- und genetischen Effekten auf Körpergewicht und Körpermaße beim Deutschen Schäferhund

Analysis of systematic environmental and genetic effects on body weight and body measurements in German shepherd dogs

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Zusammenfassung

In der Hundezucht ist die Erteilung der Zuchterlaubnis an die Einhaltung bestimmter Grenzwerte bei den Körpermaßen gebunden, die entsprechend dem Zuchtziel im Rassestandard festgelegt werden. Ziel dieser Studie war es deshalb, die Bedeutung systematischer Einflussfaktoren für die bei der Körung erfassten Körpermerkmale beim Deutschen Schäferhund (DSH) zu quantifizieren und genetische Parameter zu schätzen. Dazu wurden die Körpermerkmale Widerristhöhe, Brusttiefe, Brustumfang und Gewicht bei 36.028 gekörten DSH der Geburtsjahrgänge 1992-2003 untersucht. Geburtsjahr, Geburtsmonat und Landesgruppenklasse waren für die untersuchten Merkmale von signifikanter Bedeutung. Das Köralter war für die Widerristhöhe und Brusttiefe für beide Geschlechter und den Brustumfang nur für die Rüden signifikant. Der Inzuchtkoeffizient zeigte zu Widerristhöhe und Brusttiefe eine signifikante nichtlineare Beziehung. Die Schätzung genetischer Parameter im linearen Tiermodell erfolgte mittels Residual Maximum Likelihood (REML) unter Berücksichtigung der Verwandtschaftsmatrix von 53.429 Hunden. Die uni- und bivariaten Analysen wurden geschlechtsübergreifend und getrennt nach Geschlecht durchgeführt. Die Heritabilität in der geschlechterübergreifenden Auswertung betrug für das Körpergewicht 0,27 ± 0,01 und für die Widerristhöhe 0,41 ± 0,01. Für die Brusttiefe und den Brustumfang lagen die Heritabilitätsschätzwerte mit Werten von 0,20 ± 0,01 und 0,13 ± 0,01 niedriger. Die Hündinnen zeigten bei der nach

Geschlecht getrennten Analyse für alle Merkmale höhere Heritabilitäten als die Rüden. Die genetischen Korrelationen zwischen Rüden und Hündinnen waren für alle Merkmale mit Werten von 0,91 bis 0,98 sehr hoch. Die hohen genetischen Korrelationen weisen darauf hin, dass die Selektion auf Körpermerkmale beide Geschlechter gleichmäßig beeinflusst und den Geschlechtsdimorphismus nicht verstärkt.

Schlüsselwörter: Hund, Widerristhöhe, Brustumfang, Brusttiefe, Gewicht, Heritabilität, Korrelation

Summary

In dog breeding permission for breeding is only given when the body measurements of the dog are within the lower and upper limits which are defined in the breed standard. Therefore, the objective of this study was to analyse the systematic and genetic effects on body weight and body measurements recorded at licensing in German shepherd dogs (GSD) over a period of 10 years. The data included withers and chest height, chest circumference and body weight from 36,028 breeding dogs born between 1992 and 2003. Birth year, month of birth and region were significant for the traits analysed. Age at breeding approval was significant for the body measurements withers height and chest height and only significant for male dogs for chest circumference. Inbreeding coefficient was significant as a nonlinear covariate for withers and chest height. The genetic parameters were estimated in linear animal models using residual maximum likelihood (REML) and the relationship matrix of 53,429 dogs. Uni- and bivariate analyses were performed for both sexes together and separately for males and females. Heritability estimates for both sexes together were 0.41 ± 0.01 for withers height and 0.27 ± 0.01 for body weight. For the other traits studied, heritability estimates were lower with values of 0.20 ± 0.01 for chest height and 0.13 ± 0.01 for chest circumference. In the separate analyses for male and female dogs, heritability estimates were higher for females. Additive genetic correlations were at 0.91 to 0.98 between corresponding traits in males and females.

The high genetic correlations indicate that selection for conformation traits equally affects both sexes and does not increase sexual dimorphism in dogs.

Key words: dog, withers height, chest height, chest circumference, weight, heritability, correlation

Einleitung

Ein wesentliches Kennzeichen der Rassenvielfalt der Hunderassen ist die sehr unterschiedliche Körpergröße. Die einzelnen Hunderassen entwickelten sich nach Körpergröße und Körpermerkmalen sehr differenziert, um die an sie gestellten Aufgaben erfüllen zu können. Somit sind mit Körpergröße und Körperproportionen auch häufig funktionelle Eigenschaften verbunden. Damit der Deutsche Schäferhund (DSH) als vielseitiger Gebrauchs-, Hüte- und Dienstgebrauchshund eingesetzt werden kann, ist eine Selektion auf Körpergröße notwendig. Für den Deutschen Schäferhund (FCI Standard No. 166) sind eine Widerristhöhe von 60-65 cm für männliche Tiere und 55-60 cm für weibliche Tiere sowie ein Körpergewicht von 30-40 kg für männliche Tiere und 22-32 kg für weibliche Tiere vorgeschrieben. Bei der Körung werden deshalb Unter- und Obergrenzen für Körpermaße und das Körpergewicht festgesetzt. Diese Selektionsgrenzen werden im Rassestandard für die jeweilige Rasse festgeschrieben und könnten nur durch eine Änderung des Rassestandards geändert werden. Weder ein zu großer noch ein zu schwerer Gebrauchshund eignet sich für die vielfältigen Aufgaben und ist zudem für den Besitzer schwieriger zu führen (Helmink et al., 2001). In der Literatur finden sich überwiegend Angaben zur Entwicklung von Größenmaßen während des Wachstums, kaum dagegen zu Maßen beim ausgewachsenen Hund. Eine Schätzung des Gewichtes von ausgewachsenen Labrador Retrievern (LR) und ausgewachsenen DSH getrennt für Hündinnen und Rüden mittels Gompertz-Funktion ergab, dass die Schätzung des Gewichts für LR mit dieser Methode zu Überschätzungen führen kann (Helmink et al., 2000). Ergebnisse bezüglich des Einflusses systematischer Faktoren auf an adulten Tieren ermittelten Körpermaßen fehlen bislang. Eine Selektion auf Körpermerkmale wird durch die mittleren bis hohen Heritabilitäten für das Körpergewicht h^2 = 0,57 und die Widerristhöhe h^2 = 0,35 bei erwachsenen DSH ermöglicht (Helmink et al., 2001). Da hier die Schätzung der Heritabilitäten auf einen kleinen Datensatz von 2334 DSH zurückgeht, gilt es diese Ergebnisse anhand eines umfangreicheren Datensatzes zu überprüfen. Die Heritabilität für die Schulterhöhe beim erwachsenen Whippet wurde ebenfalls auf h^2 = 0,35 geschätzt (Meissen, 1996). Bei fast allen Hunderassen besteht ein deutlicher Geschlechtsdimorphismus, der sich u.a. in größeren Körpermaßen und höheren Körpergewichten bei Rüden ausdrückt. Diesem Geschlechtsdimorphismus wird bei der Zuchtwahl ebenfalls Rechnung getragen, indem für Rüden und Hündinnen unterschiedlich hohe Grenzwerte für die Körpermaße und das Körpergewicht festgelegt werden. Würde dieser Geschlechtsdimorphismus durch unterschiedliche Genwirkungen bedingt, so müssten die genetischen Parameter zwischen den Geschlechtern verschieden sein und es müssten sich auch genetische Korrelationen um Null zwischen den Körpermaßen der beiden Geschlechter ergeben. Ziel dieser Studie war es die Bedeutung verschiedener systematischer Faktoren zu quantifizieren und genetische Parameter für Körpermaße beim DSH zu schätzen. Aufgrund des bekannten und auch am vorliegenden Datenmaterial nachvollziehbaren Geschlechtsdimorphismus wurden sämtliche Auswertungen auch getrennt für Rüden und Hündinnen durchgeführt (Allard et al., 1998). Einer Studie an Portugiesischen Wasserhunden zufolge lässt sich dieser durch eine Interaktion zwischen einem Quantitativen Merkmalsgenort (QTL) auf dem X-Chromosom und einem QTL auf dem Hundechromosom 15 erklären (Chase et al., 2005). Aus diesem Grund sollten auch die genetischen Korrelationen für die Körpermaße und das Körpergewicht zwischen den beiden Geschlechtern untersucht werden, um mögliche zwischen den Geschlechtern bestehende antagonistischen Genwirkungen erkennen zu können.

Material und Methoden

Daten

Die in dieser Studie verwendeten Daten wurden von dem Verein für Deutsche Schäferhunde e.V. (SV), Augsburg, zur Verfügung gestellt. Abstammungsdaten lagen für die vom SV registrierten Deutschen Schäferhunde (DSH) der Geburtsjahre 1985-2006 entsprechend der Ahnentafeln und den Daten aus dem jährlich erscheinenden Zuchtbuch des SV vor. Sie enthielten für 547.356 Hunde Angaben zu Zuchtbuchnummer, Name, Zwingername, Wurfdatum und Geschlecht sowie Zuchtbuchnummer von Vater und Mutter. Kördaten lagen für 36.028 gekörte DSH der Geburtsjahre 1992-2003 mit Angaben zu Zuchtbuchnummer, Geschlecht, Wurfdatum, Körmeister, Kördatum, Körklasse, Widerristhöhe, Brusttiefe, Brustumfang und Gewicht vor.

Statistische Analyse

Aus der Kördatei berücksichtigt wurden Tiere, die in den Jahren 1992-2003 geboren wurden und zum Körzeitpunkt älter als 366 Tage und jünger als 6 Jahre waren. Hunde, zu denen Angaben wie Zuchtbuchnummer, Körpermaße, Vater-, Mutter- oder Geburtsinformationen fehlten, blieben bei den Auswertungen unberücksichtigt. Wurden Tiere mehrmals bei Körungen vorgestellt, ging der jeweils aktuellste Datensatz in die Analyse ein. Von den 36.028 gekörten Tieren (Tab. 1) waren 40 % männlich und 60 % weiblich. Insgesamt beinhaltete das Datenmaterial Hunde aus 7.262 Zwingern sowie 7.479 Vollgeschwistergruppen. Beurteilt wurden die Hunde von 180 verschiedenen Körmeistern aus 20 verschiedenen Landesgruppen. Die Landesgruppen sind weitgehend entsprechend den Bundesländern gegliedert. Zusätzlich wurde eine Pseudolandesgruppe definiert, die alle ausländischen Tiere beinhaltete. Über- und Unterschreitungen der im Rassestandard vorgegebenen Widerristhöhe von bis zu 1 cm lassen eine Ankörung in Körklasse 2 zu, bei Abweichungen von mehr als 1 cm wird der Hund nicht mehr gekört. Im vorhandenen Datenmaterial wurden 27,1 % der Tiere mit Körklasse 2 bewertet.

Für die verwendeten Auswertungsmerkmale Widerristhöhe, Brusttiefe, Brustumfang und Gewicht wurden zunächst die Einflüsse von Geschlecht, Geburtsjahr, Geburtsmonat, Landesgruppe, Alter bei der Körung, Inzuchtkoeffizient, Wurfgröße, Körmeister, Zwinger und Mutter mittels Varianzanalysen auf Signifikanz getestet. Der Körmeister wurde als zufälliger Effekt behandelt, da die Zuteilung der Körmeister für die Körung nach dem Zufallsprinzip erfolgte. Der Inzuchtkoeffizient wurde mit der Prozedur INBREED von SAS, Version 9.2 (Statistical Analysis System, SAS Institute, Cary, NC, USA, 2008) berechnet. In dem endgültigen Modell für die Varianzanalyse wurden nur die Effekte berücksichtigt, die in den einfachen und multiplen Varianzanalysen signifikant waren. Die Varianzanalysen wurden mit der Prozedur MIXED von SAS, Version 9.2, durchgeführt. Der Effekt der Geschlechter wurde bei geschlechtsübergreifenden Auswertungen als fixer Effekt berücksichtigt. Nur der zufällige Effekt des Körmeisters wurde in das endgültige Modell der Varianzanalyse aufgenommen, da dieser Effekt im Vergleich mit den anderen zufälligen Effekten von Zwinger und Mutter die größte Varianz aufwies und eine signifikante Bedeutung hatte. Nachfolgend ist das endgültige Modell für die Varianzanalyse getrennt nach Geschlechtern dargestellt:

$$Y_{ijklmnopq} = \mu + GJK_i + GM(GJK)_{ij} + LGK_k + LG(LGK)_{kl} + GJK*LGK_{ik} + b_1*KA_m + b_2*\ln(KA)_m + b_3*(\ln(KA))^2_m + b_4*WG_n + b_5*WG^2_n + b_6*\ln(WG)_n + b_7*(\ln(WG))^2_n + b_8*INZ_o + b_9*\ln(INZ)_o + b_{10}*(\ln(INZ))^2_o + km(LG)_{lp} + e_{ijklmnopq}$$

wobei $Y_{ijklmnopq}$ das jeweilige Körpermaß des ijklmnopq–ten Tieres und μ die Modellkonstante repräsentiert. Fixe Effekte waren die Geburtsjahrgangsklasse GJK_i (i= 1-6;1992-1993, 1994-1995, 1996-1997, 1998-1999, 2000-2001, 2002-2003), der Geburtsmonat (GM) innerhalb Geburtsjahrgangsklasse $GM(GJK)_{j,}$ j=1-12; Januar - Dezember), die Landesgruppenklasse LGK_k (k=1-3; Ost-, Westdeutschland, Pseudolandesgruppe), die Landesgruppe innerhalb Landesgruppenklasse $LG(LGK)_l$, (l=1-20) und die Interaktion zwischen Geburtsjahrgangsklasse und Landesgruppenklasse. Als Kovariable wurde das Köralter (KA) in Tagen (linear, logarithmisch und logarithmisch-quadratisch), die Wurfgröße (WG, linear, quadratisch, logarithmisch, logarithmisch-quadratisch) sowie der Inzuchtkoeffizient (INZ, linear, logarithmisch, logarithmisch-quadratisch) berücksichtigt, wobei $b_{1\text{-}10}$ die zugehörigen Regressionskoeffizienten darstellen. Als zufälliger Effekt ging der Körmeister innerhalb Landesgruppe (km(LG), p=1-180) in das Modell ein. Die zufälligen Restfehler werden durch $e_{ijklmnopq}$ dargestellt.

Die Schätzung genetischer Parameter im linearen Tiermodell erfolgte multivariat mittels Residual Maximum Likelihood (REML) und dem Programm VCE (variance component estimation), Version 5.1.2 (Kovač et al., 2003). Hierfür wurde das o.g. Modell durch die zufälligen Effekte der permanenten Umwelt der Zwinger zw_q (q=1-7.262) und Mutter innerhalb Zwinger (r=1-18.186) sowie durch den zufälligen additiv-genetischen Effekt des Tieres a_s (s=1-53.429) ergänzt. Es wurden alle verfügbaren Abstammungsinformationen von 53.429 Hunden einbezogen, die maximal neun Generationen umfassten, darunter 6.175 Basistiere. Die Pedigreevollständigkeit betrug in der 3. Ahnengeneration ca. 96%, in der 4. Ahnengeneration ca. 54%.

Die Heritabilität wurde als Quotient aus der additiv-genetischen Varianz (σ^2_a) und der phänotypischen Varianz (Summe der Varianzen aller zufälligen Effekte) geschätzt. Die genetischen Korrelationen (r_g) ergaben sich aus der additiv-genetischen Kovarianz zweier Merkmale (KOV) und deren additiv-genetischer Varianzen: $r_g = KOV/(\sigma_{a1} \times \sigma_{a2})$.

Ergebnisse

Für die ausgewerteten Merkmale Widerristhöhe, Brusttiefe, Brustumfang und Gewicht hatte der Geschlechtseffekt einen signifikanten Einfluss mit einer Irrtumswahrscheinlichkeit von p<0,01. Im Beobachtungszeitraum lagen die Least-Square Mittelwerte (LSM) der Rüden bei 64,3 cm ± 0,02 für Widerristhöhe, 29,8 cm ± 0,05 für Brusttiefe, 80,4 cm ± 0,01 für Brustumfang und 36,3 kg ± 0,04 für das Körpergewicht. Die LSM für Hündinnen zeigten Werte von 59,2 cm ± 0,02 für Widerristhöhe, 29,8 cm ± 0,05 für Brusttiefe, 80,4 cm ± 0,1 für Brustumfang und 28,9 ± 0,04 für das Körpergewicht. Alle getesteten Effekte hatten einen signifikanten Einfluss auf die Ausprägung eines oder mehrerer Merkmale (Tab. 2). Die fixen Effekte Geburtsjahresklasse und Geburtsmonat innerhalb Geburtsjahresklasse waren für alle vier Körpermerkmale signifikant, die Landesgruppenklasse ebenfalls

für alle vier Körpermerkmale mit Ausnahme der Brusttiefe bei Rüden und des Brustumfangs bei Hündinnen. Der Inzuchtkoeffizient hingegen war nur für Widerristhöhe und die Brusttiefe für jeweils einen nichtlinearen Regressionskoeffizienten signifikant. Die Landesgruppe innerhalb Landesgruppenklasse hatte eine signifikante Bedeutung für die Widerristhöhe, den Brustumfang (Rüden) und das Körpergewicht (Hündinnen). Die Interaktion zwischen Geburtsjahresklasse und Landesgruppenklasse war für Brusttiefe und Brustumfang signifikant. Das Köralter war für Widerristhöhe und Brusttiefe für beide Geschlechter und den Brustumfang nur für die Rüden signifikant. Die Wurfgröße war für die Widerristhöhe und das Körpergewicht signifikant.
Die LS-Mittelwerte der Merkmale Widerristhöhe und Körpergewicht unterschieden sich zwischen Rüden und Hündinnen innerhalb Geburtsjahrgangsklassen und den Landesgruppen in Ost- und Westdeutschland zu Beginn des Untersuchungszeitraums sehr deutlich (Tab. 3). Von der Geburtsjahresklasse 1992/1993 bis 1996/1997 war ein Anstieg bei beiden Geschlechtern zu verzeichnen, bevor die LSM für beide Merkmale bis 2002/2003 wieder abfielen. Die Körpermaß- und Körpergewichtsentwicklung nach Landesgruppen getrennt nach Ost und West verlief für Rüden und Hündinnen unterschiedlich. Rüden erreichten 1996/1997 für die Merkmale Widerristhöhe und Körpergewicht den höchsten LS-Mittelwert. Diese Entwicklung war in ost- und westdeutschen Landesgruppen gleich. In den folgenden Jahren nahmen die LS-Mittelwerte wieder ab. Waren die Rüden in Ostdeutschland in den Jahren 1992-1997 größer, so waren die Hündinnen signifikant kleiner als in Westdeutschland, danach näherten sich die LS-Mittelwerte für das Merkmal Widerristhöhe in den ost- und westdeutschen Landesgruppen an. Widerristhöhe und Brusttiefe waren bei jüngeren Tieren größer. Mit höheren Inzuchtkoeffizienten nahmen die Merkmale Widerristhöhe, Brusttiefe, Brustumfang und Körpergewicht zu. Je mehr Hunde pro Wurf geboren wurden, desto geringer war die Widerristhöhe, Brusttiefe, Brustumfang und das Körpergewicht dieser Tiere.
Die relativen Varianzanteile zwischen Körmeistern zeigten für die Merkmale Körpergewicht mit 1,3 – 1,7 % und Widerristhöhe mit 2,1 – 3,6 % die niedrigsten

Werte und für das Merkmal Brusttiefe die höchsten Werte mit 10,5 – 11,5 % (Tab. 4).

Die für die Merkmale Widerristhöhe, Brusttiefe, Brustumfang und Körpergewicht geschätzten Heritabilitäten, die genetischen und residualen Varianzen sind in Tab. 5 dargestellt. Die höchsten Heritabilitäten im Bereich von h^2 = 0,41 bis 0,47 wurden für das Merkmal Widerristhöhe geschätzt. Für alle Merkmale wurden bei den Hündinnen höhere Heritabilitäten geschätzt als für die entsprechenden Merkmale bei den Rüden. Die Heritabilitätsschätzwerte lagen für das Merkmal Körpergewicht bei h^2 = 0,27 (Rüden) und 0,34 (Hündinnen) und für das Merkmal Brusttiefe bei h^2 = 0,21 (Rüden) und 0,27 (Hündinnen). Für den Brustumfang ergaben sich insgesamt niedrigere Heritabilitäten für Rüden (h^2 = 0,15) und für Hündinnen (h^2 = 0,17). Aufgrund der großen phänotypischen Varianz war die additiv-genetische Varianz für die Merkmale Brustumfang und Körpergewicht geschlechtsübergreifend höher (σ_a^2 = 1,41-2,11) als für die Merkmale Widerristhöhe und Brusttiefe (σ_a^2 = 0,30-0,40). Mit Ausnahme der Widerristhöhe sind die additiv-genetische und residuale Varianz für Rüden höher als für Hündinnen (Tab. 5). Die genetischen Korrelationen zwischen den untersuchten Merkmalen waren zwischen 0,67 und 0,89, die genetischen Korrelationen für die jeweiligen Merkmale zwischen Rüden und Hündinnen bewegten sich zwischen 0,91 und 0,98 (Tab. 6).

Diskussion

Die Körpergröße sollte bei DSH bestimmte Grenzen weder über- noch unterschreiten, damit der Hund seine Aufgaben im Gebrauchshundewesen optimal erfüllen kann. Der SV ist aktuell bestrebt die Widerristhöhenmessungen aller auf Zuchtschauen vorgeführten Hunde zu intensivieren, um einer Körpermaßabweichung entgegenzuwirken und den Züchter für die Einhaltung der Größengrenzen zu sensibilisieren. Bisher liegen keine Erkenntnisse bezüglich der Körpermerkmalsentwicklung erwachsener DSH vor, deshalb wurden im Rahmen dieser Studie 36.028 DSH über einen Zeitraum von 10 Jahren untersucht. In vergleichbaren früheren Untersuchungen standen deutlich weniger Daten zur

Verfügung, nämlich Informationen zu 2.334 Hunden der Rasse DSH aus 18 Jahren (Helmink et al., 2001) bzw. 3.111 Whippets aus 16 Jahren (Meissen, 1996).
Adulte Hunde, die aufgrund von Maßabweichungen nicht gekört wurden, gingen nicht mit in die vorliegende Studie ein. Untersucht wurde damit kein Querschnitt der gesamten Schäferhundpopulation, sondern Tiere, die für die Zucht ausgewählt wurden. Es ist deshalb zu erwarten, dass die Varianzen für die Körpermaße unterschätzt wurden. Andererseits ist nicht davon auszugehen, dass die genetische Parameterschätzung dadurch erheblich beeinträchtigt wurde, da sowohl Tiere mit zu großen und zu kleinen Werten ausgeschlossen wurden, und dieser Prozentsatz nicht allzu groß sein dürfte. Deshalb kann man innerhalb der durch den Rassestandard vorgegebenen Grenzen Erkenntnisse für die Gesamtpopulation ableiten. Denn nur gekörte Hunde kommen auch selbst wieder zum Zuchteinsatz und beeinflussen die Körperentwicklung der zukünftigen Nachkommen. Bezogen auf die zugelassene Widerristhöhe wurde anhand der Rohmittelwerte deutlich, dass der DSH die obere Größengrenze nahezu erreicht hat. Sollten Rüden, um in Körklasse 1 gekört zu werden, minimal 60 cm und maximal 65 cm groß sein, so waren sie im Mittel 64,4 cm groß. Hündinnen sollten eine Widerristhöhe von 60 cm nicht überschreiten und waren im Mittel 59,2 cm groß. Für die einbezogenen Tiere betrug die Brusttiefe wie gefordert 45-48 % der Widerristhöhe. Das Körpermerkmal Brustumfang ist laut Rassestandard nur fehlerhaft, wenn eine bestimmte Form wie Flachrippigkeit oder ein tonnenförmiger Brustkorb vorliegt. Eine Umfangsüber- oder Unterschreitung führt jedoch nicht zum Zuchtausschluss. Hündinnen zeigten mit im Mittel 29,0 kg eine Annäherung an die obere Körpergewichtsgrenze, Rüden lagen mit 36,5 kg im mittleren zugelassenen Bereich (22-30 kg für Hündinnen, 30-40 kg für Rüden, von Stephanitz, 1991).
Bei der Auswertung der Daten wurden zunächst systematische Einflussfaktoren ermittelt, die Auswirkungen auf die Ausprägung der Körpermaße beim DSH zeigten. Als fixer systematischer Einflussfaktor ging die Geburtsjahresklasse mit in das Modell ein. Die berechneten LS-Mittelwerte zeigten eine ansteigende Entwicklung für die Merkmale Widerristhöhe und Gewicht von 1992/1993 bis 1996/1997. Der darauf folgende Abfall der LS-Mittelwerte bis zur Geburtsjahresklasse 2002/2003 lag

in der Veränderung der Zuchtziele des SV ab etwa 1995 begründet (Lux, persönliche Mitteilung, 2007). So waren ab 1996/1997 wieder kleinere und leichtere Hunde erwünscht. Ostdeutsche Hündinnen waren vergleichsweise kleiner als westdeutsche Hündinnen, ostdeutsche Rüden hingegen größer als westdeutsche. Der Geschlechtsdimorphismus war in Ostdeutschland in den Jahren 1992-1997 somit deutlich stärker ausgeprägt als in Westdeutschland. Eine weniger starke Ausprägung des Geschlechtsdimorphismus in Westdeutschland resultierte nicht aus einer offiziellen Formulierung eines neuen Zuchtziels. Dennoch wurden hier Hunde bevorzugt, deren Exterieurmerkmale eher dem Rassestandard entsprachen. Diese Hunde waren gleichzeitig größer, eine deutliche Größendifferenz zwischen Rüden und Hündinnen verschwand. Der Wendepunkt der Körpergrößenentwicklung lag erst ca. 7 Jahre nach Wiedervereinigung, weil Züchter aus dem Osten zunächst mit ihren Mutterlinien weiterzüchteten und zunehmend Rüden aus dem Westen Deutschlands nutzten, bevor sich beide Populationen im Zeitraum 1998-2003 anglichen. Jüngere Rüden und Hündinnen wiesen bei der Körung eine höhere Widerristhöhe und einen größeren Brustumfang auf als ältere Tiere, während im Körpergewicht keine Unterschiede zu sehen waren. Die Ursache für diese nichtzufällige Altersverteilung der Tiere ist wahrscheinlich darin begründet, dass die Besitzer hochwüchsige Tiere möglichst früh zur Körung vorstellten, damit die zulässigen Obergrenzen für die Widerristhöhe bei der Körung nicht überschritten werden. Die älteren zur Körung vorgestellten Hunde hingegen zeigten ein langsameres Wachstum und wurden dementsprechend erst bei höherem Alter zur Körung vorgestellt. Somit spiegelt der Effekt des Köralters nicht die Entwicklung der Tiere wider, sondern ist als zuchtmanagementbedingter Faktor zu interpretieren. Der im Vergleich zu den Hündinnen deutlich größere Brustumfang bei den jungen und sich schnell entwickelnden Rüden scheint geschlechtspezifisch bedingt zu sein. Als zufälliger Faktor wurde der Körmeister berücksichtigt, wodurch die Restvarianz abnahm, und damit bei der Berechnung der genetischen Parameter die Heritabilität anstieg. Mit dem Effekt des Körmeisters wurden die individuellen Unterschiede zwischen den Beurteilern und damit auch zufällige Messfehler erfasst. Da in den Modellen für die Schätzung genetischer Parameter auch der Zwinger, die Mutter und der additiv-genetische Effekt des Tieres berücksichtigt wurden, sollten keine Effekte durch die bei der Körung vorgestellten Hunde in dem Effekt des Körmeisters enthalten sein. Für das Merkmal Widerristhöhe und Körpergewicht waren die relativen Varianzanteile zwischen den Körmeistern geringer, und damit die Messgenauigkeit für diese Merkmale höher als für Brusttiefe und Brustumfang. Unter Berücksichtigung des Standardfehlers lag die in der vorliegenden Studie geschätzte Heritabilität für Widerristhöhe von h^2 = 0,41 ± 0,01 im ähnlichen Wertebereich wie die von Helmink et al. (2001) geschätzte Heritabilität von h^2 = 0,35 ± 0,08. Auch für den Whippet ergab sich für die Schulterhöhe eine etwas niedrigere Heritabilität von h^2 = 0,35 (Meissen, 1996) als bei der vorliegenden Studie. Die Heritabilität für das Körpergewicht von DSH Rüden und Hündinnen gemeinsam lag dagegen mit h^2 = 0,27 niedriger als von Helmink et al. (2001) angegeben (h^2 = 0,50 ± 0,08). Die Varianz zwischen den Körmeistern führte vor allem bei Brusttiefe und Brustumfang zu etwas geringeren Heritabilitäten. Bei vernachlässigbarer Varianz zwischen den Körmeistern würde die Heritabilität für diese beiden Merkmale um 2-3% höher sein. Bei der Heritabilitätsschätzung getrennt nach Geschlecht zeigten Hündinnen für alle Merkmale höhere Heritabilitäten. Auch wenn Rüden und Hündinnen bei der Analyse getrennt nach Geschlecht unterschiedlich hohe Heritabilitäten zeigten, so ist von einer gemeinsamen genetischen Grundlage auszugehen und geschlechtsspezifische genetische Einflüsse sind eher von untergeordneter Bedeutung. Dies zeigen die hohen genetischen Korrelationen zwischen Rüden und Hündinnen für alle Merkmale mit 0,91 – 0,98. Da sich die Proportionen zwischen großen und kleinen DSH ähnlich verhalten, sind wie erwartet auch die genetischen Korrelationen zwischen den Körpermerkmalen mit 0,67 – 0,89 hoch. Die Heritabilität kann als wichtiger genetischer Parameter zur züchterischen Beurteilung eines Merkmals genutzt werden. Je höher die Heritabilität für Körpermerkmale ist, desto eher lässt sich ein Merkmal durch züchterische Maßnahmen, insbesondere der Selektion auf den Phänotyp, beeinflussen. Auf Grundlage der hier geschätzten Heritabilitäten und genetischen Korrelationen deutet sich an, dass die Selektion auf Körpermerkmale beide Geschlechter gleichmäßig beeinflusst und den Geschlechtsdimorphismus in den vom Rassestandard vorgegebenen Grenzen aufrechterhält. Würden durch Selektionseinflüsse die Unterschiede zwischen den Geschlechtern zunehmend vergrößert, so würden die genetischen Korrelationen zwischen den Geschlechtern nicht in der hier vorgefundenen Höhe sein, sondern deutlich näher bei Null liegen. Weiterhin zeigten die Analysen der genetischen Varianzen, dass die Hündinnen eine deutlich größere genetische Streuung der Widerristhöhe als die Rüden aufwiesen und somit die Hündinnen in dem vorgegebenen Wertebereich des Rassestandards stärker streuen als die Rüden. Die Hündinnen hätten somit auch ein genetisches Potenzial zu einer Veränderung zu größeren Körpermaßen. Bei Freigabe dieser geschlechtsspezifischen Grenzwerte wäre deshalb vermutlich damit zu rechnen, dass sich die zwischen den Geschlechtern bestehenden Unterschiede in den Körpermaßen verringern würden.

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Tabelle 1: Übersicht über das analysierte Datenmaterial

Anzahl der gekörten Hunde	36.028
Anzahl der Rüden	14.415
Anzahl der Hündinnen	21.613
Anzahl der Väter	5.429
Anzahl der Mütter	15.450
Anzahl der Zwinger	7.262
Anzahl der Vollgeschwistergruppen	7.479
Körklasse 1	26.276
Körklasse 2	9.752
Wurfgröße 1-4	12.962
Wurfgröße 5-8	19.523
Wurfgröße > 8	3.543
Anzahl Körmeister	180
Anzahl Landesgruppen	20

Tabelle 2: F-Werte und Irrtumswahrscheinlichkeiten der fixen Effekte und Kovariablen für Rüden (1. Zeile) für Hündinnen (2. Zeile)

Effekt	FG	Widerrist-höhe		Brust-tiefe		Brust-umfang		Körper-gewicht	
		F	P	F	P	F	P	F	P
Geburtsjahresklasse	5	4,48	<0,001	3,34	0,005	2,06	0,067	5,59	<0,001
	5	5,11	<0,001	15,30	<0,001	8,07	<0,001	7,49	<0,001
Geburtsmonat innerhalb Geburtsjahresklasse	138	1,53	<0,001	1,22	0,038	1,28	0,017	1,38	0,002
	138	2,67	<0,001	1,67	<0,001	1,52	<0,001	2,29	<0,001
Landesgruppenklasse	2	4,38	0,013	1,84	0,159	9,31	<0,001	28,54	<0,001
	2	13,31	<0,001	9,29	<0,001	0,63	0,534	9,83	<0,001
Landesgruppe innerhalb Landesgruppenklasse	17	2,12	0,005	1,10	0,348	1,73	0,031	1,12	0,322
	17	3,17	<0,001	0,80	0,693	1,25	0,216	1,62	0,050
Geburtsjahresklasse x Landesgruppenklasse	10	1,26	0,247	4,00	<0,001	2,47	0,006	1,61	0,096
	10	1,35	0,199	9,63	<0,001	3,36	<0,001	1,76	0,062
Köralter -linear	1	18,49	<0,001	13,35	<0,001	7,62	0,006	2,51	0,113
	1	13,80	<0,001	12,02	<0,001	0,96	0,328	1,30	0,254
-(log)	1	19,24	<0,001	12,99	<0,001	6,94	0,008	2,21	0,137
	1	35,89	<0,001	10,61	<0,001	0,67	0,413	0,99	0,321
-(log)²	1	15,95	<0,001	11,16	<0,001	5,72	0,017	2,28	0,131
	1	-	-	-	-	0,72	0,397	1,33	0,249
Wurfgröße -linear	1	6,94	0,008	2,72	0,099	3,36	0,067	14,54	<0,001
	1	2,35	0,126	0,02	0,885	0,49	0,484	4,23	0,040
-quadratisch	1	5,46	0,019	2,86	0,091	4,06	0,044	16,57	<0,001
	1	3,07	0,080	0,10	0,751	0,43	0,511	4,36	0,037
-(log)	1	3,57	0,059	2,18	0,140	3,98	0,046	23,61	<0,001
	1	3,86	0,050	0,43	0,513	1,21	0,272	9,29	0,002
-(log)²	1	7,66	0,006	2,08	0,150	2,28	0,131	10,42	0,001
	1	1,29	0,255	0,05	0,817	0,23	0,633	2,89	0,089
Inzuchtkoeffizient -linear	1	0,16	0,692	1,28	0,259	0,51	0,474	0,43	0,512
	1	0,05	0,823	1,65	0,200	0,12	0,724	0,58	0,446
-(log)	1	2,86	0,091	0,64	0,425	0,04	0,835	0,37	0,542
	1	2,58	0,108	8,50	0,004	0,05	0,819	0,08	0,775
-(log)²	1	4,99	0,026	0,18	0,675	0,25	0,614	0,39	0,532
	1	5,59	0,018	11,94	<0,001	0,19	0,667	0,08	0,778

Die Kovariable $\log^2$ Köralter wurde wegen zu großer Standardfehler für Widerristhöhe und Brusttiefe bei den Hündinnen aus dem Modell entfernt.

Tabelle 3: Least-Square Mittelwerte für die Merkmale Widerristhöhe, Brustumfang, Brusttiefe und Körpergewicht nach den Landesgruppen in Ost- und Westdeutschland sowie getrennt nach Rüden und Hündinnen

Geschlecht	Widerristhöhe (cm)		Brusttiefe (cm)		Brustumfang (cm)		Körpergewicht (kg)	
Geburtsjahr	West	Ost	West	Ost	West	Ost	West	Ost
Rüden								
1992/1993	64,35 ± 0,03	64,44 ± 0,06	29,81 ± 0,07	29,51 ± 0,15	80,96 ± 0,15	79,87 ± 0,33	36,50 ± 0,09	35,51 ± 0,20
1994/1995	64,39 ± 0,03	64,44 ± 0,07	29,85 ± 0,07	29,74 ± 0,15	81,07 ± 0,16	79,73 ± 0,33	36,71 ± 0,09	35,64 ± 0,20
1996/1997	64,42 ± 0,03	64,52 ± 0,07	29,86 ± 0,07	30,03 ± 0,15	81,02 ± 0,16	80,17 ± 0,33	36,89 ± 0,09	36,26 ± 0,20
1998/1999	64,36 ± 0,03	64,45 ± 0,07	29,70 ± 0,07	29,86 ± 0,15	80,77 ± 0,16	79,82 ± 0,33	36,79 ± 0,09	36,00 ± 0,20
2000/2001	64,29 ± 0,03	64,46 ± 0,06	29,77 ± 0,07	30,09 ± 0,14	80,59 ± 0,16	79,83 ± 0,32	36,71 ± 0,10	35,95 ± 0,19
2002/2003	64,29 ± 0,04	64,32 ± 0,07	29,76 ± 0,08	30,06 ± 0,16	80,41 ± 0,18	79,83 ± 0,35	36,51 ± 0,12	35,66 ± 0,22
Hündinnen								
1992/1993	59,27 ± 0,02	59,00 ± 0,05	27,44 ± 0,05	27,06 ± 0,11	74,31 ± 0,14	73,63 ± 0,27	28,95 ± 0,06	28,61 ± 0,12
1994/1995	59,27 ± 0,02	59,03 ± 0,05	27,44 ± 0,05	27,34 ± 0,11	74,56 ± 0,14	73,96 ± 0,27	29,14 ± 0,06	28,70 ± 0,12
1996/1997	59,27 ± 0,02	59,11 ± 0,05	27,43 ± 0,06	27,55 ± 0,11	74,57 ± 0,14	74,20 ± 0,27	29,21 ± 0,06	28,88 ± 0,12
1998/1999	59,26 ± 0,03	59,08 ± 0,05	27,40 ± 0,06	27,58 ± 0,11	74,42 ± 0,14	74,53 ± 0,27	29,27 ± 0,07	28,86 ± 0,12
2000/2001	59,20 ± 0,03	58,99 ± 0,05	27,39 ± 0,06	27,66 ± 0,11	74,07 ± 0,14	74,03 ± 0,26	29,21 ± 0,07	28,88 ± 0,12
2002/2003	59,16 ± 0,03	59,04 ± 0,05	27,34 ± 0,06	27,43 ± 0,11	74,16 ± 0,15	73,90 ± 0,27	29,18 ± 0,08	28,45 ± 0,13

Tabelle 4: Varianzen zwischen Körmeistern und relative Anteile an der Gesamtvarianz mit ihren Standardfehlern für die Merkmale Widerristhöhe, Brustumfang, Brusttiefe und Körpergewicht insgesamt sowie getrennt nach Geschlecht

Merkmal	Gesamt	Rüden	Hündinnen
Varianzen zwischen den Körmeistern			
Widerristhöhe	0,019 ± 0,001	0,026 ± 0,004	0,017 ± 0,002
Brusttiefe	0,193 ± 0,013	0,256 ± 0,018	0,154 ± 0,014
Brustumfang	1,034 ± 0,022	1,120 ± 0,031	1,043 ± 0,031
Körpergewicht	0,095 ± 0,003	0,145 ± 0,008	0,075 ± 0,005
Relativer Anteil der Varianz zwischen den Körmeistern an der Gesamtvarianz			
Widerristhöhe	0,024 ± 0,003	0,036 ± 0,004	0,021 ± 0,003
Brusttiefe	0,108 ± 0,011	0,115 ± 0,011	0,105 ± 0,010
Brustumfang	0,094 ± 0,008	0,089 ± 0,008	0.105 ± 0,009
Körpergewicht	0,014 ± 0,002	0,017 ± 0,003	0,013 ± 0,002

Tabelle 5: Additiv-genetische und residuale Varianzen sowie Heritabilitäten mit ihren Standardfehlern für die Merkmale Widerristhöhe, Brustumfang, Brusttiefe und Körpergewicht insgesamt und getrennt nach Geschlecht

Merkmal	Gesamt	Rüden	Hündinnen
Additiv-genetische Varianz			
Widerristhöhe	0,32 ± 0,00	0,29 ± 0,01	0,35 ± 0,01
Brusttiefe	0,36 ± 0,01	0,40 ± 0,01	0,35 ± 0,01
Brustumfang	1,44 ± 0,02	1,61 ± 0,03	1,41 ± 0,03
Körpergewicht	1,85 ± 0,02	2,11 ± 0,04	1,78 ± 0,03
Residualvarianz			
Widerristhöhe	0,42 ± 0,00	0,39 ± 0,01	0,41 ± 0,01
Brusttiefe	1,18 ± 0,01	1,51 ± 0,02	0,92 ± 0,01
Brustumfang	8,05 ± 0,02	9,30 ± 0,04	6,90 ± 0,03
Körpergewicht	4,42 ± 0,01	5,48 ± 0,03	3,51 ± 0,02
Heritabilität			
Widerristhöhe	0,41 ± 0,01	0,43 ± 0,01	0,47 ± 0,01
Brusttiefe	0,20 ± 0,01	0,21 ± 0,01	0,27 ± 0,01
Brustumfang	0,13 ± 0,01	0,15 ± 0,01	0,17 ± 0,01
Körpergewicht	0,27 ± 0,01	0,28 ± 0,01	0,34 ± 0,01

Tabelle 6: Genetische Korrelationen (r_g) mit Standardfehlern zwischen den sich entsprechenden Merkmalen bei Rüden und Hündinnen sowie zwischen den Merkmalen Widerristhöhe, Brusttiefe, Brustumfang und Körpergewicht

Merkmale		r_g
Widerristhöhe Rüden	– Widerristhöhe Hündinnen	0,95
Brusttiefe Rüden	– Brusttiefe Hündinnen	0,98
Brustumfang Rüden	– Brustumfang Hündinnen	0,91
Körpergewicht Rüden	– Körpergewicht Hündinnen	0,91
Widerristhöhe	– Brusttiefe	0,78
Widerristhöhe	– Brustumfang	0,77
Widerristhöhe	– Körpergewicht	0,71
Brusttiefe	– Brustumfang	0,89
Brusttiefe	– Körpergewicht	0,67
Brustumfang	– Körpergewicht	0,82

Standardfehler: 0,01-0,02

CHAPTER 3

Analysis of genetic and environmental influences on body traits and their relationships with canine hip dysplasia in German shepherd dogs

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Analysis of genetic and environmental influences on body traits and their relationships with canine hip dysplasia in German shepherd dogs

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Summary

The aim of this study was to investigate whether body measurements including withers height (WH) and body mass index (BMI) have an influence on canine hip dysplasia (CHD) and if possible genetic relationships could have an impact for selection against CHD. The data for this analysis included body measurements of 31,398 dogs and CHD scores of 105,756 German shepherd dogs (GSD) born between 1992 and 2003. The pedigree contained 141,100 animals including ancestors for up to four generations. Genetic parameters were estimated in bivariate linear animal models using Gibbs sampling. Distribution of CHD scores in progeny by WH and BMI of their parents indicated that there is no obvious correlation between CHD in progeny and body measurements of their parents. Heritabilities were estimated at $h^2 = 0.18 \pm 0.01$ for CHD, $h^2 = 0.49 \pm 0.04$ for WH and $h^2 = 0.17 \pm 0.02$ for BMI. A slightly positive genetic correlation among CHD score and BMI was found. However, the low genetic correlations between CHD and body measurements let expect only a small influence of WH and BMI on CHD.

Keywords dog; German shepherd dog; body weight; body measurements; body mass index; heritability; correlation

Introduction

Canine hip dysplasia (CHD) is one of the most important hereditary skeletal diseases in many dog breeds including German shepherd dogs (GSD) as CHD limits the long term motility and working performance of dogs (Distl *et al.* 1991). Breeding programs have been developed to reduce the prevalence of CHD. As early as in 1966 a selection program was initiated to reduce CHD in the GSD population.

Phenotypic records of hip dysplasia scores based on radiographs of both hip joints were employed for selection of parents. Sires and dams were not allowed for breeding if their CHD scores were above an agreed threshold. The disadvantage of this selection method was that breeding progress was slow and particularly in small populations success of these breeding programs was not always obvious (Janutta *et al.* 2008). Relative breeding values (RBV) for CHD are in use in the German population of GSD for planning of matings since 1999. Janutta *et al.* (2008) analysed the genetic and phenotypic trends for GSD born between 1985 and 2003 with the result that selection schemes based on RBV should result in a larger breeding progress than selection on phenotypic records of parents. Selection response may also benefit from utilization of information on genetically correlated traits which help to characterize CHD disposition. To further optimize the selection strategy against CHD, it might be useful to investigate body measurements and their influence on CHD. The relevance of body weight, height at the withers (WH) and Body Mass Index (BMI) as risk factors for developing CHD have been suggested in different studies, with body weight significantly increasing the risk to develop CHD in Labrador Retrievers and GSD (Sallander *et al.* 2006; Smith *et al.* 2001). Furthermore, CHD has been reported to occur with high prevalence in large, fast growing and heavy dogs, when simultaneously selecting for appearance (Mäki *et al.* 2005). To investigate the relationship between CHD and body measurements of different dog breeds, Comhaire & Snaps (2008) analysed data of 156 dog breeds scored for CHD and with known withers height, body weight and BMI. A significantly positive correlation of $r = 0.63$ was found between the breed prevalence of CHD and BMI using an across-breed analysis. For GSD, conformation data is routinely collected in the course of dog inspections for breeding approval and this data was used to analyse whether the reported interbreed relationship corresponds to within-breed relationships among CHD and body measurements within the German population of GSD. Therefore, the objective of this study was to show the relationship among body measurements of parents with the CHD phenotype of their progeny and to estimate heritabilities for body measurements as well their correlations with CHD.

Materials and methods

The data used in this analysis was provided by the German Shepherd Dog Breeding Association (Verein für Deutsche Schäferhunde e.V.) in Augsburg, Germany and consisted of 31,398 dogs with conformation evaluations. These dogs were born between 1992 and 2003. Withers height (WH) and body weight (BW) were used to calculate the body mass index (BMI) as the ratio of BW in kg with squared WH in m. Only dogs older than 366 days and younger than 6 years at the date of licensing and with complete information on date of birth, parents and body measurements were included in this study. When dogs were presented several times for licensing only the last result was considered. Information on CHD scores was available for 105,756 GSD born between 1992 and 2003. CHD scores followed the official evaluation scheme of the Fédération Cynologique Internationale (FCI) ranging from CHD A, normal hip joints without signs of CHD, to CHD E, severely dysplastic joints. The pedigree file consisted of 574,356 registered animals born between 1985 and 2006.

Statistical Analysis

Previous analyses demonstrated genetic correlations between males and females in body traits close to one and therefore, sex specific analyses seemed not necessary (Dammann *et al.* 2009). Because it could not be ruled out that body measurements were affected by the CHD status of the dogs and in order to preclude this possible bias, two sets of genetic analyses were performed. In the first set, all available information on WH and BMI was used, whilst in the second set only information on respective body measurements of dogs scored as CHD grade A was used but CHD scores of all dogs. In each analysis, pedigree information on four generations was included resulting in a relationship matrix of in total 141,100 animals among which were 14,438 base animals. The fixed effects of sex of the dog, birth year, month of birth, region, regional subdivision, litter size, inbreeding coefficient and age at licensing, and the random effects of kennel, judge, dam and litter were tested for significance in preliminary analyses using the MIXED procedure of SAS, Version 9.2 (SAS Institute, Cary, NC, USA, 2008). Inbreeding coefficients were estimated using all available pedigree information using PEDIG (Boichard 2002). According to the results of the analysis of variance the following models were used for (co)variance component estimation:

CHD score:

$$y_{ijtuv} = \mu + S_i + Y_j + a_t + m_u + e_{ijtuv}$$

Body measurements (WH, BMI):

$$y_{ijklmnopqrstuv} = \mu + S_i + Y_j + MON(Y)_{jk} + RC_l + RC(Y)_{jl} + REG_m + LS_n + IB_o + b_1\, age_p + b_2\, \ln(age_p) + b_3\, (\log(age_p))^2 + k_q + dam(k)_{qr} + j_s + a_t + m_u + e_{ijklmnopqrstuv}$$

with $y_{i...v}$ = trait value for body measurements WH or BMI or CHD grade, S_i = fixed effect of the sex (I = male, female), Y_j = fixed effect of birth year classes (j = 1992/1993, 1994/1995, 1996/1997, 1998/1999, 2000/2001, 2002/2003), $MON(Y)_{jk}$ = fixed effect of birth month within birth year (jk = 1 – 72), RC_l = fixed effect of the region class (l = Western Germany, Eastern Germany, other countries), $RC(Y)_{jl}$ = fixed effect of the region class within birth year (jl = 1 – 18), REG_m = fixed effect of regional subdivision (m = 1 - 20), LS_n = fixed effect of litter size classes (n = 1 – 3, with classes of 1 – 4, 5 – 8, > 8 dogs per litter), IB_o = fixed effect of inbreeding coefficient classes (o = 1 – 3, with inbreeding coefficients of 0.0, 0.001 – 0.015, >0.015), age_p = age at licensing as linear, logarithmic and logarithmic-quadratic covariate with regression coefficients b_1, b_2 and b_3, $dam(k)_{qr}$ = random effect of the dam within kennel (qr = 1 – 15,182), k_r = random effect of the kennel (q = 1 – 5,894), j_s = random effect of the judge (s = 1 – 102), a_t = random additive genetic effect of the animal (t = 1 – 141,100), m_u =random maternal genetic effect (m = 1 – 20,831), and $e_{i...V}$ = random residual effect.

Genetic parameters were estimated in bivariate linear animal models using Gibbs sampling with the program MTGSAM (Van Tassell & Van Vleck 1996) which assumes normal distributions of random and residual effects and uses flat priors for the fixed effects. A starting value of 0.5 was chosen for the additive genetic and the residual variance, and a proper prior using an inverse Wishart distribution with minimum shape parameter (v_{IW} = 6) was adopted for the genetic variance matrix. The total length of the Gibbs chain was set to 505,000, and the first 5,000 rounds were discarded as burn-in. Visual inspections of sample plots revealed that this length of burn-in was always sufficient to achieve convergence. Results from each 1000th round of Gibbs sampling were saved to calculate the posterior estimates. Heritabilities were calculated from variances (σ^2) and covariances (cov) as follows:

$h_a^2 = \sigma_a^2/(\sigma_a^2 + 2\, cov_{am} + \sigma_m^2 + \sigma_j^2 + \sigma_k^2 + \sigma_{dam(k)}^2 + \sigma_e^2)$ for BMI and WH and

$h_a^2 = \sigma_a^2/(\sigma_a^2 + 2\, cov_{am} + \sigma_m^2 + \sigma_e^2)$ for CHD, with h_a^2 = heritability, σ_a^2 = additive genetic variance of the animal, cov_{am} = covariance between the additive genetic effect of the animal and additive genetic maternal effect, σ_m^2 = additive genetic maternal variance, σ_j^2 = variance among judges, σ_k^2 = variance among kennels, $\sigma_{dam(k)}^2$ = variance among dams within kennels, σ_e^2 = residual variance. To allow direct comparison with previous studies, analogous bivariate genetic analyses including CHD and BMI were performed using the same model for BMI and simplified models for CHD and running Gibbs chains of 105,000 rounds with results from each 500th round being saved. In the models only the fixed effect of month of birth was considered together with random animal and maternal genetic effects or only with random animal genetic effect. Breeding values for CHD were subsequently compared using the CORR procedure of SAS.

Results

The mean values for the analysed body measurements were 61.23 cm ± 2.68 (55.0 - 66.0 cm) for WH and 84.93 cm ± 6.92 (58.33 - 120.04 kg/m^2) for BMI. Among the dogs born in 1992 – 2003, 63.4% were scored as CHD grade A, 22.9% as CHD grade B, 9.3% as CHD grade C, 3.6% as CHD grade D and 0.9 % as CHD grade E. The Pearson correlation coefficients were low and positive between WH and CHD (0.0111, $P < 0.05$) and close to zero between BMI and CHD (-0.0029, $P = 0.61$).

The distribution of CHD scores in dogs of birth years 1992 - 2003 by the body measurements of their parents are shown in Table 1 for WH and Table 2 for BMI. Regardless of the mating constellations with respect to WH and BMI of sire and dam, mean CHD scores of offspring varied mostly from 1.30 to 1.38 with standard deviations in the order of 0.58 to 0.61 and ranges of mostly 1 to 3. A clear trend for CHD scores of progeny according to the body measurements of the parents was not visible. Estimated variance and covariance components from the bivariate analyses using the full model with all available information on body measurements being considered are given in Table 3. Analyses using body measurements of dogs scored as CHD grade A only gave very similar results for heritabilities and correlations among the direct genetic and maternal genetic effects. The correlations between the direct additive genetic and the additive genetic maternal effect were at 0.13 for CHD, 0.12 for WH and 0.57 for BMI. Maternal heritabilities were all very low (range 0.013 - 0.042, SE < 0.01) when compared to the heritabilities for the direct component of the animal, which were 0.18 for CHD, 0.49 - 0.51 for WH and 0.16 - 0.17 for BMI (SE < 0.05) in both analyses. The additive genetic covariances between CHD and WH and between CHD and BMI were both small, but different from zero. Genetic correlations from analyses using WH of all CHD scored dogs including CHD grade A - E were close to zero (-0.003) as opposed to a genetic correlation of 0.09 including only dogs scored as CHD A. The genetic correlations between CHD and BMI were 0.07 (all dogs) and 0.05 (BMI only from CHD A dogs), respectively. The phenotypic correlation was -0.028 between CHD and WH, and -0.071 between CHD and BMI.

Using the simplified model with both animal and maternal genetic effects for CHD, additive genetic heritability decreased slightly to 0.17 (SE 0.01), whilst exclusion of the maternal genetic effect from the model resulted in an increase of the heritability to 0.20 (SE 0.01). Comparisons of breeding values for CHD estimated under the different models revealed very small differences with Pearson correlation coefficients ≥ 0.99.

Discussion

The aim of this study was to investigate if there is a genetic correlation between CHD and body measurements such as withers height and body mass index. In the German shepherd dog breeding association selection against CHD was introduced as early as 1966. Mean CHD scores for offspring showed a low variation even if parents had high or low values for WH and BMI. The distribution of CHD scores indicated that there is no obvious correlation between the body measurements of the parents and the CHD scores of their progeny. However, Comhaire & Snaps (2008) analysed the relationships between CHD and body measurements across different dog breeds and found a significant correlation of 0.63 between the breed prevalence of CHD and the breed average for the BMI. Our results implicate that across-breed relationships between CHD and BMI can not be directly transferred to the German population of GSD. Across-breed CHD-BMI correlations may result from genetic divergence of dog breeds according to selection for size, behaviour and other breed characteristics and genetic linkage of these traits with alleles and haplotypes encoding for CHD. Therefore, across-breed correlations reflect antagonistic or synergistic effects of loci nearly fixed in a significant number of dog breeds and thus, these across-breed correlations are atmost genetically caused. Thus, these across-breed correlations should be compared with genetic correlations within breeds and not with phenotypic correlations within breeds. The within-breed genetic correlations in the GSD indicate an increased risk for CHD with larger body traits and so far this result is in agreement with Comhaire & Snaps (2008). On the other hand, our results indicate that an across-breed correlation is not identical with genetic correlations within breeds and this lowers the value of across-breed analyses for conclusions within breeds. Due to the narrow limits of variation in body measurements within a breed, we did not expect close genetic correlations for these traits.

In previous reports there are conflicting statements on the phenotypic relationships of WH, BW and BMI with CHD. On the one hand, body weight of the individual dog has been considered as a significant risk factor for CHD (Sallander *et al.* 2006; Smith *et al.* 2001), and CHD has been reported to be more often prevalent in large, fast growing and heavy dogs, when simultaneously selecting for appearance (Mäki *et al.* 2005). On the other hand, no significant influence of BW on CHD (Popovitch *et al.* 1995; Ohlerth *et al.* 1998; Goddard and Mason 1982; Wienrich 1973) and no significant influence of WH on CHD (Wienrich 1973) have been reported for different dog breeds. Our results were in agreement with these latter studies. In an investigation on Rottweilers, Maimer (2003) analysed the data of 31,854 dogs born in 1985 – 1995 and found a slightly negative phenotypic correlation between WH and CHD ($r = -0.052$) and between BW and CHD ($r = -0.034$).

Heritability estimates for CHD were slightly lower than estimates reported for GSD in previous studies (Hamann *et al.* 2003; Henricson *et al.* 1972; Leppänen *et al.* 2000; Lingaas and Heim 1987). Heritability estimates for height at the withers were higher than estimates found in other reports which ranged between 0.35 and 0.41 (Dammann *et al.* 2009; Helmink *et al.* 2001; Meissen 1996). The fact that our estimates were higher than previously reported estimates may be at least in parts due to the different methods used. It has been shown that Gibbs sampling may lead to some overestimation of variances particularly in case of moderate to high heritabilities (Van Tassell & Van Vleck 1996). There is no report on heritability estimations of BMI in the dog. Maternal heritabilities were much smaller than heritabilities of the animal corresponding to previously reported results for CHD in the German population of GSD (Hamann *et al.* 2003).

The genetic correlations between CHD and WH and between CHD and BMI were very small. Underestimation because of some yet unknown influence of CHD affection on body measurements was precluded by comparison with parallel analyses including only body measurements of dogs of CHD grade A. Both sets of analyses revealed very similar results for BMI but not for WH. Given the low phenotypic and genetic correlations between body measurements and CHD it can be concluded that WH and BMI may not be very useful as accessory traits for selection against CHD. Using the across-breed correlations and our results, increase of WH and BMI are genetically positively correlated with CHD and thus development of body measurements has to be controlled and breeding of GSD should aim to keep variance of body measurements as low as possible and within the breed standard.

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Table 1 Distribution of CHD scores in dogs of birth years 1992 - 2003 by withers heights (WH) of their parents. Numbers of offspring given in the first line, mean CHD scores with standard deviations (SD) in the second line and minimum and maximum CHD scores in the third line

Phenotype of the sire	Phenotype of the dam					
	< 57.0 (n = 133)	57.0 - 58.0 (n = 459)	58.0 - 590 (n = 1,144)	59.0 - 59,5 (n = 395)	59.5 - 60,0 (n = 1,712)	> 60.0 (n = 28)
< 62.0 (n = 31)	n = 3 1.67 ± 0.58 (1 - 2)	n = 20 1.10 ± 0.31 (1 - 2)	n = 25 1.24 ± 0.44 (1 - 2)	n = 3 1.67 ± 0.15 (1 - 3)	n = 24 1.50 ± 0.78 (1 - 3)	n = 4 1.00 ± 0.00 (1)
62.0 - 63.0 (n = 114)	n = 52 1.29 ± 0.54 (1 - 3)	n = 162 1.35 ± 0.58 (1 - 3)	n = 269 1.35 ± 0.58 (1 - 3)	n = 71 1.30 ± 0.57 (1 - 3)	n = 244 1.36 ± 0.59 (1 - 3)	n = 14 1.00 ± 0.00 (1)
63.0 - 64.0 (n = 383)	n = 153 1.29 ± 0.58 (1 - 3)	n = 409 1.35 ± 0.61 (1 - 4)	n = 1,004 1.30 ± 0.55 (1 - 3)	n = 312 1.33 ± 0.57 (1 - 3)	n = 1,154 1.35 ± 0.59 (1 - 3)	n = 28 1.36 ± 0.62 (1 - 3)
64.0 - 64.5 (n = 179)	n = 38 1.34 ± 0.58 (1 - 3)	n = 186 1.35 ± 0.63 (1 - 3)	n = 528 1.37 ± 0.62 (1 - 3)	n = 176 1.38 ± 0.61 (1 - 3)	n = 851 1.33 ± 0.59 (1 - 3)	n = 11 1.55 ± 0.69 (1 - 3)
64.5 - 65.0 (n = 689)	n = 159 1.34 ± 0.61 (1 - 3)	n = 727 1.35 ± 0.58 (1 - 4)	n = 2,383 1.36 ± 0.60 (1 - 4)	n = 884 1.36 ± 0.60 (1 - 3)	n = 4,154 1.38 ± 0.60 (1 - 4)	n = 62 1.47 ± 0.72 (1 - 3)
> 65.0 (n = 22)	n = 11 1.36 ± 0.50 (1 - 2)	n = 20 1.35 ± 0.59 (1 - 3)	n = 38 1.32 ± 0.53 (1 - 3)	n = 15 1.33 ± 0.62 (1 - 3)	n = 73 1.41 ± 0.64 (1 - 3)	n = 2 1.00 ± 0.00 (1)

Table 2 Distribution of CHD scores in dogs of birth years 1992 - 2003 by body mass indices (BMI) of their parents. Numbers of offspring given in the first line, mean CHD scores with standard deviations (SD) in the second line and minimum and maximum values in the third line

Phenotype of the sire	Phenotype of the dam					
	< 75.0 (n = 425)	75.0 - 80.0 (n = 666)	80.0 - 85.0 (n = 1,417)	85.0 - 90.0 (n = 833)	90.0 - 95.0 (n = 371)	> 95.0 (n = 159)
< 75.0 (n = 20)	n = 21 1.48 ± 0.68 (1 - 3)	n = 23 1.48 ± 0.67 (1 - 3)	n = 52 1.27 ± 0.53 (1 - 3)	n = 21 1.43 ± 0.68 (1 - 3)	n = 7 1.29 ± 0.49 (1 - 2)	n = 3 1.00 ± 0.00 (1)
75.0 - 80.0 (n = 65)	n = 56 1.36 ± 0.67 (1 - 3)	n = 96 1.40 ± 0.59 (1 - 3)	n = 163 1.28 ± 0.53 (1 - 3)	n = 101 1.38 ± 0.60 (1 - 3)	n = 55 1.25 ± 0.52 (1 - 3)	n = 13 1.23 ± 0.60 (1 - 3)
80.0 - 85.0 (n = 226)	n = 140 1.41 ± 0.56 (1 - 3)	n = 269 1.38 ± 0.61 (1 - 3)	n = 533 1.42 ± 0.63 (1 - 3)	n = 299 1.31 ± 0.52 (1 - 3)	n = 135 1.33 ± 0.53 (1 - 3)	n = 53 1.34 ± 0.52 (1 - 3)
85.0 - 90.0 (n = 529)	n = 623 1.35 ± 0.61 (1 - 3)	n = 982 1.37 ± 0.58 (1 - 3)	n = 2,117 1.37 ± 0.61 (1 - 4)	n = 1,138 1.33 ± 0.58 (1 - 3)	n = 561 1.37 ± 0.62 (1 - 3)	n = 216 1.41 ± 0.63 (1 - 3)
90,0 - 95,0 (n = 412)	n = 559 1.36 ± 0.60 (1 - 3)	n = 880 1.36 ± 0.58 (1 - 3)	n = 1,852 1.34 ± 0.60 (1 - 4)	n = 1,087 1.37 ± 0.62 (1 - 4)	n = 453 1.36 ± 0.61 (1 - 3)	n = 185 1.32 ± 0.56 (1 - 3)
> 95.0 (n = 166)	n = 163 1.35 ± 0.57 (1 - 3)	n = 266 1.34 ± 0.57 (1 - 3)	n = 569 1.31 ± 0.57 (1 - 3)	n = 348 1.36 ± 0.59 (1 - 4)	n = 177 1.36 ± 0.60 (1 - 3)	n = 53 1.34 ± 0.48 (1 - 2)

Table 3 Additive genetic variances (σ_a^2) and covariances (cov_{am}) between the additive genetic individual and additive genetic maternal component, heritabilities (h_a^2) and genetic correlations (r_g), additive genetic maternal variances (σ_m^2) and maternal heritabilities (h_m^2), residual variances (σ_e^2) and phenotypic (σ_p^2) variances with their standard errors (SE) for canine hip dysplasia (CHD), body mass index (BMI) and withers height (WH) of dogs with CHD scores A-E or with CHD score A only from bivariate analyses

Variance components	CHD score	WH	CHD score	BMI
Body measurements of dogs with CHD grade A to C (n = 31,398)				
σ_a^2	0.134 ± 0.009	0.363 ± 0.024	0.135 ± 0.009	6.747 ± 0.624
cov_{am}	-0.001 ± 0.007		0.065 ± 0.043	
σ_m^2	0.010 ± 0.002	0.031 ± 0.006	0.010 ± 0.002	0.119 ± 0.059
σ_e^2	0.622 ± 0.006	0.395 ± 0.013	0.621 ± 0.006	29.450 ± 0.449
σ_p^2	0.766 ± 0.005	0.824 ± 0.017	0.766 ± 0.005	39.211 ± 0.442
h_a^2	0.175 ± 0.011	0.491 ± 0.035	0.177 ± 0.011	0.168 ± 0.015
h_m^2	0.013 ± 0.003	0.042 ± 0.008	0.013 ± 0.003	0.003 ± 0.001
r_g	-0.003 ± 0.034		0.069 ± 0.045	
r_p	-0.028 ± 0.001		-0.071 ± 0.004	
Body measurements of dogs with CHD grade A (n = 21,992)				
σ_a^2	0.133 ± 0.009	0.366 ± 0.027	0.134 ± 0.009	6.291 ± 0.713
cov_{am}	0.019 ± 0.012		0.065 ± 0.043	
σ_m^2	0.010 ± 0.002	0.031 ± 0.006	0.010 ± 0.002	0.209 ± 0.085
σ_e^2	0.622 ± 0.006	0.395 ± 0.015	0.621 ± 0.006	30.144 ± 0.558
σ_p^2	0.765 ± 0.005	0.822 ± 0.018	0.765 ± 0.005	39.179 ± 0.460
h_a^2	0.175 ± 0.012	0.507 ± 0.040	0.175 ± 0.012	0.154 ± 0.017
h_m^2	0.013 ± 0.002	0.044 ± 0.009	0.013 ± 0.002	0.003 ± 0.001
r_g	0.086 ± 0.052		0.051 ± 0.069	

CHAPTER 4

Evaluation of the predictive value of pedigree breeding values for canine hip dysplasia in the German shepherd dog

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Evaluation of the predictive value of pedigree breeding values for canine hip dysplasia in the German shepherd dog

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Summary

The aim of this study was to evaluate the predictive value of pedigree breeding values (PBV) for canine hip dysplasia (CHD) as it is currently practiced in the German population of German shepherd dogs (GSD). The ability of PBV to predict offspring phenotypes was compared with selective breeding based on the CHD phenotype of parents. Official scores for CHD of 184,489 GSD from birth years 1985 to 2007 were included in the analyses. Pedigree information on eight generations was considered for prediction of PBV resulting in a relationship matrix of 200,853 dogs. PBV explained 2-3% of the phenotypic variance of CHD in GSD. In contrast to PBV, the proportion of phenotypic variance explained by the parents` phenotypes was lower than 1%. Therefore, selection using PBV maybe preferable over mass selection but selection response for CHD is limited.

Keywords: canine hip dysplasia; genetic evaluation; pedigree breeding values; phenotypic variance.

Introduction

Canine hip dysplasia (CHD) is one of the most important skeletal diseases which has been described for many dog breeds including the German shepherd dog (GSD) (Leppänen *et al*. 2000; Hamann *et al*. 2003, Janutta et al. 2008). As early as 1966, mass selection based on radiological screening for CHD has been introduced by the Breeding association of German shepherd dogs in Germany (Verein für Deutsche Schäferhunde e.V., SV). Since that date, dogs with moderate and severe hip dysplasia are excluded from breeding. Since 1983, prediction of breeding values (BV) using Best Linear Unbiased Prediction (BLUP) has been introduced in several dog breeds. Since 1999, pedigree breeding values (PBV) for CHD are used for planning of future matings in the GSD. According to the breeding standards of the SV (SV 2008), the mean PBV of two possible mating partners should not exceed 100 to limit the risk of CHD in the future offspring. However, many investigators found that response to both phenotype and combined phenotype and PBV based selection against CHD was not satisfactory in several dog breeds including the GSD (Flückiger *et al*. 1995; Swenson *et a*l. 1997; Leppänen and Saloniemi 1999; Hamann *et al*. 2003; Janutta *et al*. 2008). The aim of this study was to evaluate the ability of PBV to predict offspring phenotypes compared with selective breeding based on the CHD phenotype of parents.

Material and methods

Results of radiographic examinations for CHD were used for this study. Phenotype information on CHD scores was available for 184,489 GSD from the birth years 1985 to 2007 and included data on date of birth, sex, sire, dam, kennel and age at examination for CHD. Phenotype data and pedigree information on all dogs was provided by the SV.

Development of CHD distribution was studied in the dogs from birth years 1985 to 2006. The proportion of CHD score availability per litter was 31.2% across all litters, and 48.9% across litters with at least one dog with known CHD phenotype. The phenotypic trend for CHD was studied using proportions of dogs classified as CHD grade A, B and C to E and mean CHD scores. For the latter, original CHD scores were expressed on a numeric scale from one corresponding to CHD grade A to five corresponding to CHD grade E. Development of mean scores was studied in all dogs and separately in dogs from litters with examination rate for CHD of up to 50% and dogs from litters with examination rate for CHD larger than 50%.

For the genetic analyses, pedigree information up to eight generations was considered, resulting in a relationship matrix comprising 200,853 dogs with 12,307 base and 188,546 non-base animals. Breeding values were predicted under the assumption of a heritability of CHD of 0.20 using Best Linear Unbiased Prediction (BLUP) with the program PEST, version 4.2 (Groeneveld 1990). This heritability estimate was chosen according to previous analyses in which variance components for CHD were estimated on the basis of CHD information on 105,756 dogs from birth years 1992 to 2003 (Dammann et al. 2009). The model currently used for the genetic evaluation for CHD in the GSD only includes the month of birth of the dog as a fixed effect together with the random additive genetic effect of the animal (Beuing 2008). The same model was employed in this study to predict pedigree breeding values (PBV) for future breeding animals:

$$y_{ijk} = \mu + MO_i + a_j + e_{ijk}$$

with y_{ijk} = CHD phenotype of the j^{th} animal, μ = model constant, MO_i = fixed effect of the month of birth (i = 1-12), a_j = random additive genetic effect of the j^{th} animal (j = 1-200,853), and e_{ijk} = random residual.

PBV include phenotypic records of the parents and all other ancestors except the phenotypic record of the proband and all other contemporaries from the same birth year and all progeny. Thus, for all dogs of each birth year PBV were predicted using all available phenotypic information and pedigree records prior to the birth year in which the probands were born. PBV were predicted for dogs born from 1986 to 2007. All these 177,625 dogs were already radiographically examined for CHD. PBV were standardized to a mean of 100 and a standard deviation of 10 using all dogs classified as CHD grade B as the reference population according to Beuing (2008). Standardization was performed such that PBV larger than 100 indicate animals more likely to show signs of CHD and PBV smaller than 100 indicate animals less likely to develop CHD.

To investigate whether the proportion of full sibs with known CHD score had an impact on the prediction of breeding values, genetic evaluation was performed with a reduced data set. In this data set only phenotypes of dogs were considered which were from full sib families with examination rate larger than 50% and had at least one examined full sib.

The efficiency of phenotype based mass selection and PBV based selection were studied by comparative analysis of distributions of CHD grades in the next offspring generation. Finally, the proportions of phenotypic variance explained by the phenotypes or PBV were calculated using the procedure GLM of the Statistical Analysis System, version 9.2 (SAS Institute, Cary, NC, USA, 2008).

Results

The development of the proportions of GSD classified as CHD grade A, B and C to E is given in Figure 1. In total, the mean proportion of dogs classified as CHD grade A was 60.7%, whilst 23.7% of the dogs were classified as CHD grade B and 15.6% were classified as CHD grade C, D or E. Between 1985 and 2006, the proportion of dogs classified as CHD grade A increased by about 0.8% per year, and the proportion of dogs classified as CHD grade C, D or E decreased by about the same amount. When dogs were born 2000 to 2001, the proportion of dogs classified as CHD grade B increased and the proportion of dogs classified as CHD grade A and C to E decreased. Mean CHD score decreased from 1.8 in 1985 to 1.4 in 2006.

The development of mean CHD scores in the dogs from birth years 1985 to 2006 is shown in Figure 2. In 1985 to 1992 there was a marked decrease of the mean CHD score which was equally seen in dogs from litters with examination rates of up to 50% and larger than 50%. However, the curve flattened afterwards, and further decrease of mean CHD score was minimal in 1992 to 2005. Distinction between litters of different examination rates for CHD revealed, that mean CHD score was consistently lower in the dogs from litters in which CHD phenotype was known for more than half of all litter mates.

For 124,605 GSD born between 1987 and 2007 CHD phenotypes of parents were available. The distribution of CHD scores in these dogs by the CHD scores of their sire and dam is given in Table 1. Matings of parents which were both free of radiographic signs of CHD (CHD grade A) led to the maximum proportion of progeny classified as CHD grade A (67.2%) and the minimum mean CHD score (1.49 ± 0.82). Less favorable mating constellations with respect to the CHD phenotype of sire and dam resulted in proportions of CHD grade A of 46.8 to 61.9% and mean CHD scores of 1.57 to 1.85 when only parents with CHD grades A to C were considered. Because breeding with dogs classified as CHD grade D is only possible in exceptional cases, very few offspring came from such matings. Mean CHD score among these dogs was 1.72 to 2.11.

For all 177,265 dogs born from 1986 and 2007 with known CHD phenotype distributions of PBV for the parents (PBV_{sire}, PBV_{dam}) and the progeny (PBV_{animal}) is given in total and by the CHD score of the progeny in Table 2. PBV of parents with progeny examined for CHD was 100 with a standard deviation of 12 in the sires and 11 in the dams. Due to the standardization on dogs with CHD grade B, mean PBV in all dogs classified as CHD grade B was 100 $\pm$ 10. Means of PBV were slightly larger than 100 in sires and dams when their progeny was classified as CHD grade B to D.

The distribution of CHD scores in the progeny is given by classes of PBV of sires and dams in Table 3. When both mating partners had PBV smaller than 80, the mean CHD score in the progeny was 1.27, with a proportion of progeny with CHD grade A of 80.0%. When one mating partner had a PBV smaller than 80, mean CHD score in the progeny increased to 1.5 and the proportion of progeny classified as CHD grade A decreased to about 65% with increasing PBV of the other mating partner. When both mating partners had PBV larger than 100, the mean CHD score in the progeny was at 1.65 to 1.89, with proportions of progeny with CHD grade A from 58.5 to 47.0%. Progeny from parents with PBV smaller than 90 had mean CHD scores from 1.27 to 1.42 and proportions from 70.2 to 80% CHD grade A.

The proportions of phenotypic variance of CHD explained by the phenotypes of their parents and their own PBV and their PBV are given in Table 4 for all progeny and by birth years. The phenotypes of the parents explained less than 1% of the variance of the CHD grade, in the offspring. Using PBV for progeny, up to 3% of the phenotypic variance of the CHD grade in the progeny could be explained. Comparison between PBV predicted on the basis of the whole or the reduced CHD data showed, that exclusion of CHD information on dogs with no examined full sib or maximally 50% of examined full sibs did not increase the proportion of explained variance of CHD. Conversely, the proportion of explained phenotypic variance decreased by about one third both across and within birth years.

Discussion

In dog breeding, selection of mating partners is based on different characteristics, such as height, appearance, obedience and health traits. CHD is one of the most important skeletal diseases limiting the working fitness of dogs regardless of their use. Accordingly, the motivation to develop breeding strategies, which reduce the number of dogs affected by CHD or at least to limit the risk of individual dogs to develop CHD is high. In the GSD, selection against CHD is practiced for decades, but mass and PBV based selection have not yet led to a satisfactory improvement of the CHD status in the German population of GSD (Janutta *et al*. 2008). So the aim of this study was to evaluate the predictive value of PBV for CHD phenotypes in comparison with phenotype based selection.

Radiographic screening for CHD is obligatory for breeding animals to get permission for breeding. The proportion of GSD dogs with known CHD phenotype has been more or less constant over the years and ranges between 30 and 40%. It is not clear whether or to which extent the available CHD phenotype data are representative for the CHD distribution in the whole German GSD population.

Over the study period of 21 years, the proportion of dogs classified as CHD grade A increased and the proportion of dogs classified as CHD grade C, D or E decreased by about 0.8 % per year. The proportion of dogs classified as CHD grade B remained constant. Therefore, introduction of PBV based selection for CHD has not led to a further improvement compared with the improvement before 1999 when selection against CHD was exclusively based on phenotypes (Janutta *et al.* 2008). In the present analysis the low correlation between parent and offspring phenotype was reflected by for example the rather low proportion of progeny with CHD grade A (67.2 %) when CHD grade A sires were mated to CHD grade A dams. Although the most favorable figures with respect to the proportion of progeny classified as CHD grade A and mean CHD score was obtained by mating sires and dams with most favorable phenotypes (CHD grade A) and the worst figures were obtained by mating sires and dams with least favorable phenotypes (CHD grades C or D), the differences between the phenotypically defined mating constellations were mostly small. A comparison of phenotypic selection and selection on the basis of PBV in the

GSD showed that PBV for CHD predicted for sires and dams are more suitable to distinguish CHD disposition of progeny groups than the parental phenotypes (Janutta *et al.* 2008). Furthermore the proportion of dogs classified as CHD grade A showed an increase of about 16% when selection based on PBV compared to phenotype based mass selection but the proportions of explained phenotypic variance, corresponding to the predictive ability with respect to offspring phenotypes, in the order of 1 to 3% explain the little success in CHD elimination. There are different factors which limit the performance of selection based on PBV. Given the sound basis of genetic evaluation, which is represented by use of phenotype information on a random sample of the population, accuracy of breeding values and therefore selection response will increase with increasing amount of information (Dietschi *et al*. 2003). However, it had not been analyzed before whether an increasing amount of information per litter or full sib family would increase the predictive value of PBV. Therefore we compared the predictive value of PBV predicted using all CHD information or only CHD information on dogs from full sib families with examination rate for CHD of more than 50% per litter. In the available data we could not see any positive effect of data restriction. The already low proportion of phenotypic variance of CHD explained by PBV further decreased when the reduced CHD data set was used for PBV prediction.

Possible reasons for the limited breeding progress with respect to CHD may be the low selection intensity and the use of selection criteria which insufficiently distinguish between favorable and unfavorable breeding animals. Currently, decisions about breeding approvals in the GSD are based on CHD phenotypes. However, our results have shown that there is no close relation between parent and offspring CHD scores. BV for CHD are used for planning of matings, but the only moderate heritability of 0.20 for CHD plus Mendelian sampling reduce the possibility to predict progeny phenotypes by PBV. Furthermore, previous analyses on the inheritance of CHD in the GSD have shown that a major gene or few major genes may be involved (Janutta *et al.* 2006; Marschall and Distl 2007). Deviation from the purely polygenic character of a trait interferes with reliable genetic evaluation. Based on the available data it is not possible to identify one main factor responsible for the limited selection response.

Selection based on PBV is more efficient than phenotype based mass selection, although the proportion of phenotypic variance of CHD explained by PBV was in the order of only 2 to 3%. This was still larger than the proportion of phenotypic variance explained by parental CHD phenotypes. Accordingly, PBV may be preferred over phenotypes to select against CHD, but further selection response is likely to be limited.

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Table 1 Distribution of CHD scores in 124,605 German shepherd dogs from birth years 1987 to 2007, for which CHD phenotypes of both of their parents were known, by CHD scores of sire and dam. The number of dogs is given in the first line, the proportion of dogs classified as CHD grade A is given in the second line, and the mean CHD score with its standard deviation and with CHD grade being expressed on a scale from 1 to 5 corresponding to the original A to E scale is given in the third line.

CHD score of the sire	CHD score of the dam			
	A (n = 15,985)	B (n = 4,930)	C (n = 1,930)	D (n = 24)
A (n = 5,283)	n = 64,413 **67.21** 1.49 ± 0.82	n = 18,737 61.89 1.57 ± 0.86	n = 6,873 58.36 1.65 ± 0.91	n = 44 59.09 1.73 ± 1.13
B (n = 2,040)	n = 20,136 61.10 1.59 ± 0.88	n = 5,832 **56.40** 1.68 ± 0.92	n = 2,286 52.41 1.75 ± 0.95	n = 13 53.85 2.00 ± 1.29
C (n = 662)	n = 4,343 57.26 1.67 ± 0.93	n = 1,453 53.41 1.73 ± 0.92	n = 447 **46.76** 1.85 ± 0.97	
D (n = 8)	n = 18 66.67 1.72 ± 1.32	n = 9 11.11 2.11 ± 0.60		n = 1 **0.00** 2.00

Table 2 Distribution of pedigree breeding values for progeny (PBV_{animal}) and their parents (PBV_{sires}, PBV_{dams}) for 177,265 progeny born between 1986 and 2007 with known CHD phenotype. The number of dogs is given in the first line, the mean PBV with its standard deviation in the second line and minimum and maximum are given in the third line.

	Mean ± SD (Minimum – Maximum)		
CHD grade	PBV_{animal}	PBV_{sires}	PBV_{dams}
A	n = 108,434 97.65 ± 10.01 (60.29 - 146.09)	n = 5,583 93.03 ± 9.47 (59.71 - 135.80)	n = 16,682 93.53 ± 9.25 (62.07 - 147.42)
B	n = 41,845 100.00 ± 10.00 (64.01 - 146.09)	n = 2,182 104.25 ± 9.58 (74.82 - 144.65)	n = 5,173 104.62 ± 9.54 (72.90 - 149.55)
C	n = 18,160 102.41 ± 9.97 (69.44 - 143.91)	n = 727 115.42 ± 9.81 (84.39 - 156.27)	n = 2,021 114.85 ± 10.20 (87.50 - 155.02)
D	n = 7,442 103.26 ± 10.04 (72.87 - 144.12)	n = 10 128.15 ± 12.16 (106.57 - 151.90)	N = 28 125.29 ± 9.95 (105.94 - 142.44)
unknown phenotype	n = 1,384 102.02 ± 10.35 (71.25 - 141.25)	n = 3,386 105.70 ± 8.25 (53.41 - 155.09)	n = 9,503 105.85 ± 7.40 (62.58 - 151.54)
A to E	n = 177,265 98.96 ± 10.17 (60.29 - 146.09)	n = 11,888 100.10 ± 11.61 (53.41 - 156.27)	n = 33,407 100.07 ± 11.25 (62.07 - 155.02)

Table 3 Distribution of CHD scores in 177,265 German shepherd dogs from the birth years 1986 to 2007 by classes of pedigree breeding values (PBV) for CHD of sires and dams. The number of dogs is given in the first line, the proportion of dogs classified as CHD grade A in the second line, and the mean CHD score with its standard deviation in the third line.

PBV class of the sire	PBV class of the dam							
	< 80 (n=1,064)	80-84 (n=2,097)	85-89 (n=3,633)	90-94 (n=4,516)	95-99 (n=4,957)	100-104 (n=4,674)	105-109 (n=7,835)	≥ 110 (n=4,631)
< 80 (n=438)	**n=1,259** **79.98** **1.27 ± 0.64**	n=1,637 77.95 1.30 ± 0.64	n=2,482 74.86 1.36 ± 0.72	n=2,612 72.63 1.39 ± 0.73	n=2,372 70.91 1.39 ± 0.72	n=2,033 71.13 1.41 ± 0.74	n=1,675 69.31 1.44 ± 0.76	n=1,902 64.98 1.51 ± 0.82
80-84 (n=770)	n=975 77.85 1.29 ± 0.61	**n=1,491** **73.17** **1.36 ± 0.68**	n=2,160 72.69 1.36 ± 0.68	n=2,495 70.70 1.43 ± 0.76	N=2,267 67.93 1.46 ± 0.79	n=1,786 65.17 1.51 ± 0.82	n=1,478 64.75 1.52 ± 0.83	n=1,736 59.91 1.62 ± 0.91
85-89 (n=1,282)	n=1,154 71.14 1.39 ± 0.72	n=2,074 71.26 1.40 ± 0.74	**n=2,788** **70.23** **1.42 ± 0.76**	n=3,141 67.81 1.46 ± 0.79	n=3,116 65.85 1.50 ± 0.82	n=2,649 63.57 1.53 ± 0.83	n=2,253 61.83 1.58 ± 0.87	n=2,412 60.61 1.59 ± 0.87
90-94 (n=1,579)	n=1,163 75.24 1.33 ± 0.64	n=1,883 70.10 1.43 ± 0.76	n=3,006 68.20 1.45 ± 0.77	**n=3,500** **67.60** **1.48 ± 0.81**	n=3,581 63.08 1.55 ± 0.84	n=3,470 62.45 1.58 ± 0.88	n=3,276 60.59 1.61 ± 0.90	n=3,651 56.31 1.70 ± 0.95
95-99 (n=1,671)	n=1,012 73.32 1.37 ± 0.70	n=1,734 67.24 1.48 ± 0.80	n=3,050 66.10 1.49 ± 0.80	n=3,462 62.65 1.57 ± 0.88	**n=3,854** **61.70** **1.57 ± 0.86**	n=3,526 58.79 1.63 ± 0.89	n=3,415 57.89 1.67 ± 0.93	n=3,977 55.34 1.71 ± 0.95
100-104 (n=1,534)	n=745 70.47 1.41 ± 0.74	n=1,400 66.50 1.50 ± 0.82	n=2,444 63.83 1.54 ± 0.86	n=3,033 63.37 1.57 ± 0.89	n=3,471 59.72 1.62 ± 0.89	**n=3,168** **58.46** **1.65 ± 0.92**	n=3,665 55.80 1.71 ± 0.96	n=4,012 53.19 1.76 ± 0.98
105-109 (n=2,855)	n=576 67.36 1.47 ± 0.78	n=1,088 62.32 1.57 ± 0.86	n=1,879 62.16 1.55 ± 0.83	n=2,669 60.13 1.60 ± 0.87	n=3,361 57.69 1.66 ± 0.91	n=3,662 56.03 1.71 ± 0.96	**n=7,083** **54.62** **1.74 ± 0.97**	n=5,104 48.57 1.85 ± 1.00
≥ 110 (n=1,759)	n=702 64.53 1.54 ± 0.85	n=1,509 62.03 1.58 ± 0.87	n=2,784 61.06 1.58 ± 0.86	n=3,850 55.38 1.70 ± 0.93	n=4,832 55.19 1.71 ± 0.94	n=4,924 51.52 1.78 ± 0.96	n=6,748 48.19 1.87 ± 1.02	**n=7,049** **46.97** **1.89 ± 1.03**

Table 4 Proportion of phenotypic variance of CHD in 177,265 German shepherd dogs from birth years 1986 to 2007 explained by the CHD phenotypes of their parents (CHD_{Sire}, CHD_{Dam}) and their pedigree breeding values estimated on the basis of the whole data set (PBV_{all}) and the reduced data set (PBV_{red}) on the basis of phenotype information on dogs which had at least one examined full sib and were from fullsib

Year of birth	Phenotypes of the parents			Breeding values of the animal	
	CHD_{sire}	CHD_{dam}	CHD_{sire} and CHD_{dam}	PBV_{all}	PBV_{red}
1986-1990 (n=43,578)	0.004	0.005	0.006	0.015	0.008
1991-1995 (n=47,173)	0.002	0.002	0.004	0.014	0.010
1996-2000 (n=43,903)	0.003	0.004	0.006	0.021	0.014
2001-2005 (n=36,407)	0.003	0.002	0.005	0.021	0.017
2006-2007 (n=6,204)	0.003	0.002	0.004	0.024	0.015
Study period, i.e. 1986-2007 (n=177,265)	0.005	0.004	0.008	0.031	0.023

Figure 1 Development of proportions of dogs classified as CHD grades A, B and C to E (phenotypic trend) in German shepherd dogs from birth years 1985 to 2006.

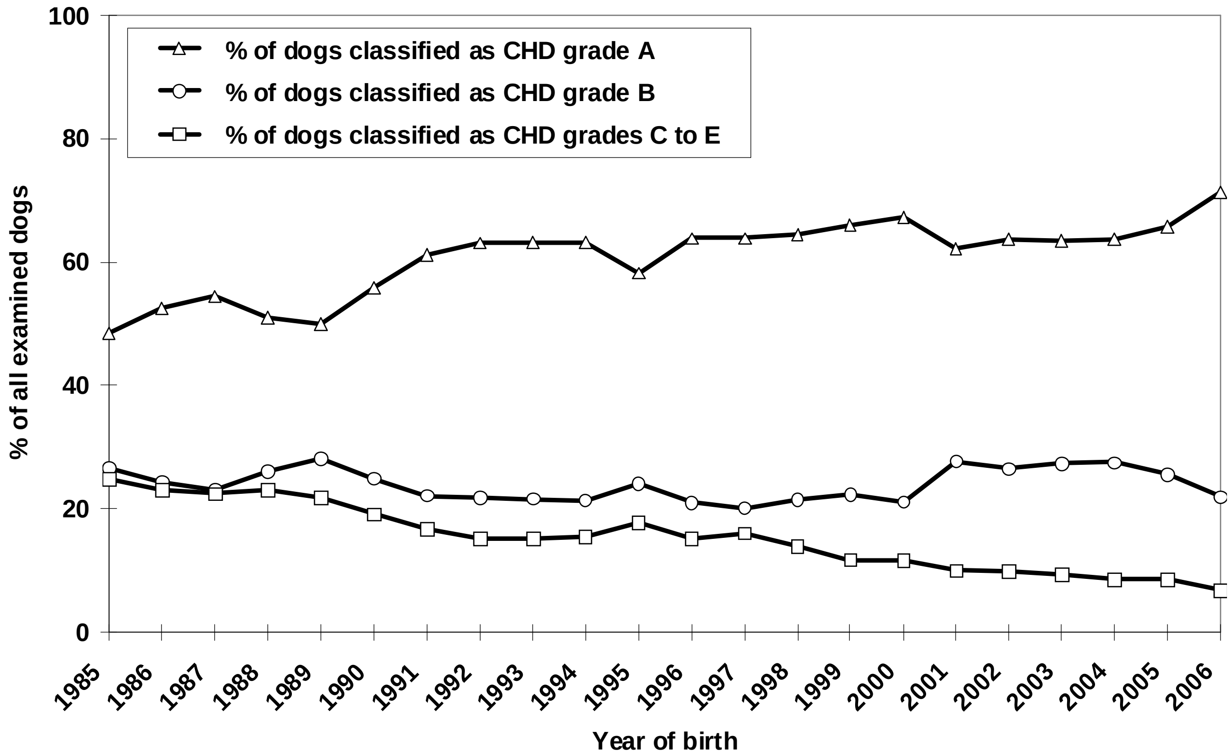
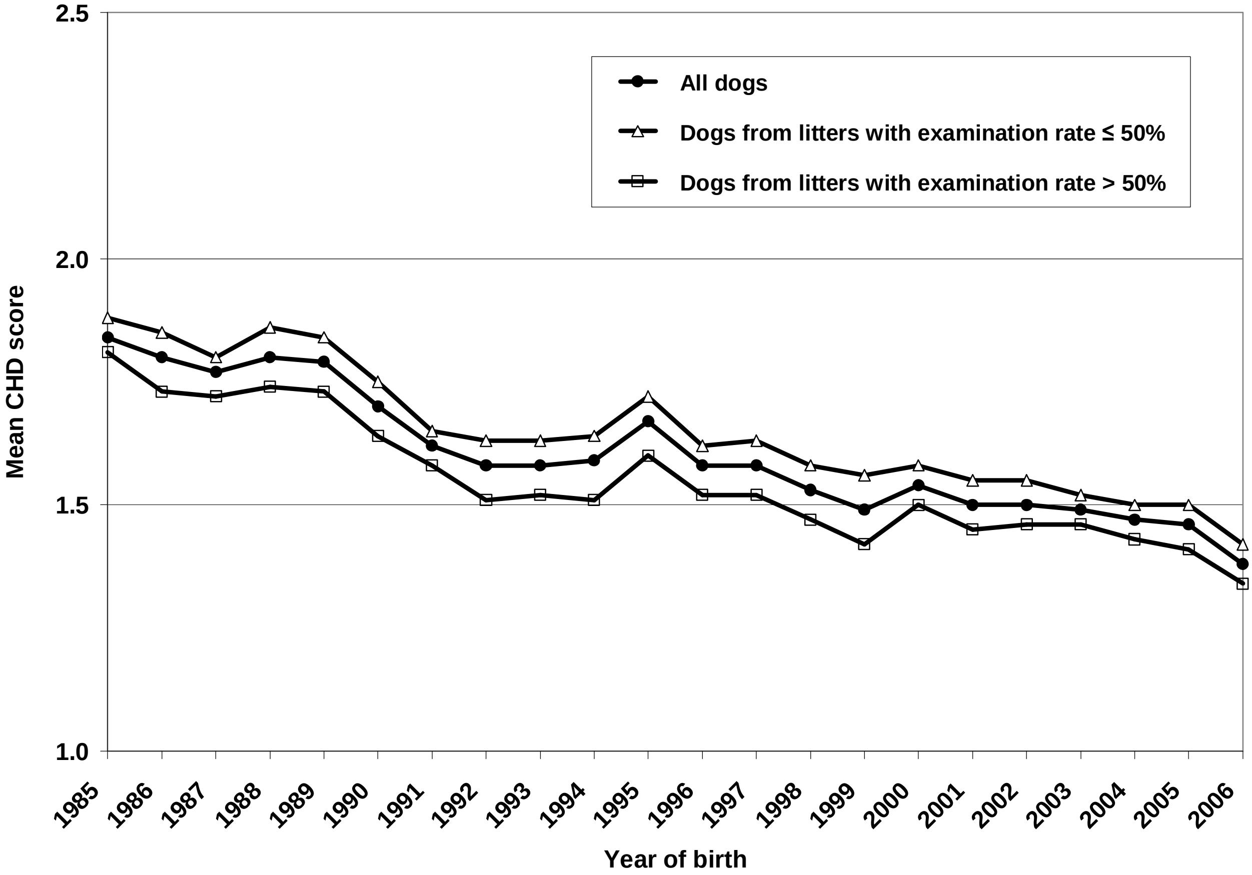


Figure 2 Development of mean CHD scores in dogs from birth years 1985 to 2006 in total and by examination rate among litter mates.



CHAPTER 5

Selection for conformation and conformational homogeneity of litters in the German shepherd dog

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Selection for conformation and conformational homogeneity of litters in the German shepherd dog

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Summary

Breeding standards of most dog breeds specify tolerable ranges of certain conformation traits. In the German shepherd dog (GSD) current means of withers height (WH) and body weight (BW) are close to the upper limits defined in their standard. Therefore, strategies to avoid further increase of size and to maximize the proportion of dogs fitting the breeding standard with respect to WH and BW were to be compared. Results of conformation evaluations from breeding approvals, arranged by the German GSD breeding association in 1994-2005, were used. Body measurements were available for 14,416 male and 21,612 female GSD from 26,155 litters. WH and body mass index (BMI), i.e. the quotient of BW and squared WH, were considered as traits to directly select for certain size and stature. Using information on 17,154 GSD from litters with at least two dogs with conformation data, within litter variances of WH (vWH) and BMI (vBMI) were defined as traits to select for conformational homogeneity of litters. Officially recorded scores of canine hip dysplasia (CHD) of all dogs were used to monitor possible side effects of conformation selection on CHD. Genetic parameters were estimated multivariately in linear animal models using Gibbs sampling. Heritabilities ranged between 0.19 and 0.41 for all traits with additive genetic correlation of -0.11 between WH and vWH and 0.11 between BMI and vBMI. Breeding values (BV) for WH and BMI were negatively correlated with -0.19 in sires and -0.17 in dams. Expected selection response was studied using relative breeding values (RBV) of parents, assuming exclusion of sires and/or dams with RBV larger than 120, and comparing means of WH, BMI and CHD score between offspring of all and selected parents. Concurrent selection for small WH and vWH was found to most efficiently reduce mean WH in males and females while having little impact on CHD distributions. Multiple trait selection for WH, vWH, BMI and vBMI was hindered by the negative genetic correlations between the traits and tended to interfere with improvement of CHD status. Use of RBV for WH and vWH for conformation selection is therefore recommended to maximize breeding success with regard to conformation and conformational homogeneity in the GSD.

Keywords: withers height, body mass index, within litter variance of conformation, expected selection response.

Introduction

In dog breeding, conformation traits represent important selection criteria. For most breeds, the breeding standards focus on the appearance of the dogs, define minima and maxima for certain body measures which are to be kept by male and female breeding animals. In this connection it should be mentioned that esthetic aspects may not only be relevant for pet and show dogs, but may also play some role in working dogs. However, in the latter functional aspects are to be considered as well. Guard dogs like the German shepherd must have a certain stature to be able to fulfill their duties, making it plausible that withers height (WH) and body weight (BW) are routinely measured in selection candidates. Other body measurements like chest width and chest depth are taken as well and many body points are subjectively scored in the GSD, but WH and BW are considered most important for the usability of the dogs. Sex-specific minima and maxima of WH and BW are therefore fixed in the breeding standard of the GSD, and selection as a breeding dog requires fitting the standard. Although BMI reflects appropriateness of BW to WH and selection on BMI should therewith be more efficient in producing dogs of favorable body proportions and stature, it is not yet used as a selection trait.

Moderate to high heritabilities of body measures provide the basis for selective breeding towards for example smaller or larger withers height. This kind of conformation selection is practiced across species, regardless of being uniparous or multiparous. However, in multiparous species similarity of siblings with regard to specific aspects of conformation may be as important as the individual phenotypes of the siblings. The risk of postnatal losses due to insufficient food supply or disease may be smaller, and raising of litters may generally be more successful in case of homogeneous than in case of inhomogeneous litters (Damgaard et al. 2003, Wolf et al. 2008). Furthermore, because juvenile differences in size and stature of individuals often persist in adulthood, small differences between litter mates may coincide with large proportions of progeny fitting the breeding standard. The proportions of dogs eligible as breeding animals and suited for their intended use represent criteria to distinguish between successful and less successful breeders. However, the genetic basis of homogeneity versus inhomogeneity of litters with regard to conformation traits has not yet been investigated in the dog. Accordingly, the genetic correlations between the most important conformation traits, that is WH and BW or BMI, on the one hand and their variance within litters on the other hand is unknown for the GSD.

Physical health is another prerequisite for usability of an individual, so monitoring of health traits has been introduced by most dog breeding organizations. In the GSD, radiographic examination for canine hip dysplasia (CHD) is obligatory for all breeding animals for more than four decades, and selection against CHD is practiced since 1966. Therefore, all studies on traits relevant for current or future selection in the GSD should also consider CHD to assure feasibility and efficiency of selection practices. The aims of this study were to estimate genetic parameters for WH and within litter variance of WH and for BMI and within litter variance of BMI and to investigate the expected responses to selection for conformation, within litter variance of conformation or both. Expected selection responses were to be expressed for the conformation traits of interest, WH and BMI, and for CHD to assess opportunities for modifications of the currently practiced selection schemes.

Material and methods

Data

Conformation data collected in the course of breeding approvals of German shepherd dogs (GSD) in Germany between 1994 and 2005 were used for this study. Information on body measurements was provided together with base and pedigree information by the German Shepherd Dog Breeding Association (Verein für Deutsche Schäferhunde e.V., SV) in Augsburg, Germany. Body measurements included withers height (WH) in centimeters and body weight (BW) in kilograms (kg), from which the body mass index (BMI) was calculated as the quotient of BW in kg and squared WH in meters (m). All WH and BW measurements were taken by judges authorized by the SV. Date and place of conformation evaluation were documented as were the judge and the regional division of the SV which organized the breeding approval. In case of repeated presentation of dogs, only the last result of conformation evaluation was considered. Base information was available for all dogs with conformation data and included specifications of sex, kennel, date of birth, sire and dam. Additional information referred to the officially recorded CHD grade of the dogs. CHD recording was according to the standard protocol which has been described elsewhere. To facilitate comparing CHD distributions and tracing CHD development under selection for conformation, the original scale of CHD grades from A to E was transformed to a five point numeric scale, with CHD score 1 corresponding to original CHD grade A, CHD score 2 corresponding to original CHD grade B and so on.

Information referred to 14,416 male and 21,612 female GSD, which were born between 1992 and 2003. In both sexes, conformation evaluation took place at the mean age of about 34 months, with age ranges of 16 to 72 month in the males and 13 to 72 months in the females. All 36,028 dogs were positively evaluated at breeding approval, i.e. received the allowance to reproduce under the SV. The distributions of dogs across litters are together with trait distributions shown in Table 1. The breeding standard of the SV request WH of 60 to 65 cm and BW of 30 to 40 kg for males and WH of 55 to 60 cm and BW of 22 to 32 kg in females (FCI standard no. 166). However, according to the SV regulations for breeding approval, minor anatomical faults may be tolerated, including minor over- or undersize. In the males of this study mean WH was 64.37 ± 0.89 cm, mean BW was 36.47 ± 2.88 kg, and mean BMI was 88.00 ± 6.38 kg/m². Corresponding means in the females of this study were 59.22 ± 0.94 cm for WH, 29.03 ± 2.42 kg for BW, and 82.75 ± 6.48 kg/m² for BMI. In both sexes, ranges of BW were considerably larger (25.0-47.0 kg in males, 20.0-41.5kg in females) than those suggested in the breeding standard. Of the 26,155 litters which were represented by at least one dog with conformation data, less than one third (7,282 litters) contributed two or more approved dogs. However, conformation information on at least two dogs per litter was required to calculate within litter variances as the squared standard deviation from the litter mean of WH (within litter variance of WH, vWH) and BMI (within litter variance of BMI, vBMI). Accordingly, the number of dogs with vWH and vBMI information was considerably smaller than the total number of dogs with conformation information, namely 17,154 dogs among which were 7,136 males and 10,018 females. Means and ranges of WH and BMI were almost identical in all dogs with conformation information and in the dogs with at least one conformation evaluated litter mate. The proportion of litters contributing both males and female dogs was 58% (n = 4,215), whilst 13% of litters (n = 926) contributed only males and 29% of litters (n = 2,141) contributed only females. Because of the sex dimorphism with regard to WH and BW, within litter variances were to be adjusted for litter size, the proportion of approved dogs in the litter and the proportion of males among the approved dogs. More than 50% of all litter mates were approved in only 30% of the litters with two or more dogs with conformation data. Maximum within litter variances were expected in litters with only two informative dogs of different gender. However, according to results of previous genetic analyses, in which genetic correlations close to unity were found between corresponding body measures of males and females (Dammann et al. 2009a), both WH and BMI were considered to represent the same traits in male and female dogs.

Estimation of genetic parameters

Genetic analyses were performed for the conformation traits WH and BMI and their within litter variances, vWH and vBMI. To limit the computational efforts, the analyses were split up into two bivariate analyses, each of which including one conformation trait and the corresponding within litter variance: (1) WH and vWH, and (2) BMI and vBMI. In both analyses pedigree information on four generations was included, resulting in a relationship matrix of in total 65,551 animals among which were 12,249 base animals.

Model development was based on the result of analyses of variance which were performed for WH, BMI, vWH and vBMI using the procedure MIXED of the Statistical Analysis System, version 9.2 (SAS Institute, Cary, NC, USA, 2008). All available pedigree information, which included up to ten generations, was used to estimate inbreeding coefficients with PEDIG (Boichard 2002). The fixed effects of month and year of birth, age at breeding approval, region and regional division of the SV organizing the breeding approval, litter size and inbreeding coefficient, and the random effects of judge, kennel, dam, dam within kennel and litter were considered for all traits. In addition, the fixed effect of the sex of the dog was considered for WH and BMI only, and the fixed effects of the proportion of approved dogs per litter and the proportion of male dogs among the approved dogs per litter were considered for vWH and vBMI only. The following models were used for (co)variance component estimation:

$$y_{ijklmnopqtuvw} = \mu + SEX_i + AGE_j + MONTH_k + YEAR_l + REG_m + RDIV_n + IBC_o + LS_p + judge_s + kennel_t + dam(kennel)_u + a_v + e_{ijklmnopqtuvw}$$

$$y_{jklmnopqrstuvw} = \mu + AGE_j + MONTH_k + YEAR_l + REG_m + RDIV_n + IBC_o + LS_p + P\_APP_q + P\_MALE_r + judge_s + kennel_t + dam(kennel)_u + a_v + e_{jklmnopqrstuvw}$$

with $y_{i...w}$ ($y_{j...w}$) = trait value for WH or BMI (within litter variance of WH or BMI), μ = model constant, SEX_i = fixed effect of the i-th sex (i = 1-2; male, female), AGE_j = fixed effect of the j-th class of age at breeding approval (j = 1-3; ≤ 24 months, 25 to 36 months, > 36 months), $MONTH_k$ = fixed effect of the k-th month of birth (k = 1-12; individual months from January to December), $YEAR_l$ = fixed effect of the l-th class of year of birth (l = 1-6; 1992/1993, 1994/1995, 1996/1997, 1998/1999, 2000/2001, 2002/2003), REG_m = fixed effect of the m-th region of breeding approval (m = 1-3; Western Germany, non-German countries, Eastern Germany), $RDIV_n$ = fixed effects of the n-th regional division of the SV organizing the breeding approval (n = 1-20; 19 individual German regional divisions of the SV, non-German regional divisions combined), IBC_o = fixed effect of the o-th class of inbreeding coefficient (o = 1-3; 0.000, 0.001-0.015, > 0.015), LS_p = fixed effect of the p-th class of litter size (p = 1-3; up to four puppies, four to seven puppies, more than seven puppies), P_APP_q = fixed effect of the q-th class of proportion of approved breeding animals in the litter (q = 1-5; < 0.20, 0.20-0.39, 0.40-0.59, 0.60-0.79, ≥ 0.80), P_MALE_r = fixed effect of the r-th class of proportion of males among the approved breeding animals in the litter (r = 1-5; < 0.20, 0.20-0.39, 0.40-0.59, 0.60-0.79, ≥ 0.80), $judge_s$ = random effect of the s-th judge (s = 1-109), $kennel_t$ = random effect of the t-th kennel (t = 1-7,267), $dam(kennel)_u$ = random effect of the u-th dam within kennel (u = 1-18,180), a_v =

random additive genetic effect of the v-th animal (v = 1-65,551), and $e_{i...w}$ ($e_{j...w}$) = random residual.

Genetic parameters were estimated in bivariate linear animal models using Gibbs sampling with the program MTGSAM (Van Tassell and Van Vleck 1996) which assumes normal distributions of random and residual effects and uses flat priors for the fixed effects. A starting value of 1.0 was chosen for the additive genetic and the residual variance, and a proper prior using an inverse Wishart distribution with minimum shape parameter (v_{IW} = 4) was adopted for the genetic variance matrix. The total length of the Gibbs chain was set to 105,000, and the first 5,000 rounds were discarded as burn-in. Visual inspections of sample plots revealed that this length of burn-in was always sufficient to achieve convergence. Results from each 500th round of Gibbs sampling were saved to calculate the posterior estimates. Heritabilities (h^2) and additive genetic correlations (r_g) were calculated for two traits 1 and 2 from respective additive genetic variances (σ_a^2), residual variances (σ_e^2) and additive genetic covariances (cov_a) as

$h_i^2 = \sigma_{ai}^2 / (\sigma_{ai}^2 + \sigma_{ei}^2)$ with i = 1, 2, and

$r_{g12} = cov_{a12} / (\sigma_{a1} * \sigma_{a2})$.

Genetic evaluation and expected response to selection

Breeding values predicted for WH, vWH, BMI and vBMI were subsequently standardized to a mean of 100 and a standard deviation of 20. In each case, the parents of informants served as the reference population. The 36,028 dogs with conformation data descended from 5,427 sires and 15,439 dams, so standardization of breeding values for WH and BMI was to the mean of 20,866 dogs of the parent generation. The 17,154 dogs with information on vWH and vBMI, i.e. from litters with at least two conformation evaluated litter mates, descended from 2,001 sires and 5,436 dams, so standardization of breeding values for vWH and vBMI was to the mean 7,437 dogs of the parent generation. The relative breeding values (RBV) were used for all further analyses.

Joint distributions of RBV for WH, vWH, BMI and vBMI were studied using the procedure CORR of SAS. Pearson correlation coefficients were calculated between respective RBV in the sires and dams of all dogs with conformation data and of the dogs from litters with at least two conformation evaluated litter mates.

The accuracy of genetic evaluation was investigated using the proportion of phenotypic variance of the traits, which was explained by the RBV predicted for the dogs itself (RBV_{ind}) or the RBV predicted for its sire (RBV_{sire}) or dam (RBV_{dam}). Coefficients of determination were estimated using the procedure GLM of SAS, considering the phenotype of the informant as dependent variable and the respective RBV as independent variable. To account for the sex dimorphism of conformation, analyses were performed under adjustment for sex for both sexes together and separately for male and female dogs, using the following model:

$y_{x\,ij} = \mu + b * RBV_{xz}(SEX_i) + e_{ij}$

with x = WH, vWH, BMI or vBMI, and z = ind, sire or dam, and

with $y_{x\,ij}$ = phenotype of the individual, μ = model constant, $RBV_{xz}(SEX_i)$ = relative breeding value for the respective trait within sex (i = male, female) as linear covariate with regression coefficient b, and e_{ij} (e_j) = random residual. In the separate analyses for male and female dogs, linear regression within sex reduced to simple linear regression on the respective RBV.

To illustrate the relation between parental RBV and offspring phenotypes, classes of RBV were defined and the distributions of offspring phenotypes for WH, BMI and CHD by the parental RBV classes for WH, vWH, BMI and vBMI were studied.

Finally, expected responses to selection based on RBV for the conformation traits, their within litter variances, or both were studied. Because we had found that in both males and females the body measurements were close to the upper limits defined in the breeding standard, excessive size as measured by WH and heavy stature as measured by BMI should be avoided in future breeding. To investigate whether the predicted RBV for WH and BMI were suitable to achieve this, we assumed exclusion of sires, dams or sires and dams with respective RBV larger than 120. Distributions of WH and BMI in the offspring of the parents with RBV of up to the defined selection limit of 120 were then compared with the distribution of WH and BMI in all conformation evaluated dogs. Expected selection response was reflected by the decrease of WH and BMI. Homogeneity of litters with respect to conformation was assumed to represent another possibility to minimize the number of dogs of extreme size or extremely heavy stature. Furthermore, selection for limited within litter variance of conformation may be applied alone or in combination with WH or BMI selection. Therefore, the same selection limit of 120 was set for RBV of vWH and vBMI, and expected response to selection with respect to WH and BMI was studied as described above. Because of the importance of CHD in the breeding of GSD, distributions of CHD were monitored in all selection scenarios studied. Selection scenarios considered between one and four traits (WH; vWH; WH and vWH; BMI; vBMI; BMI and vBMI; WH and BMI; vWH and vBMI; WH, BMI, vWH and vBMI) and selection in only one gender or both genders (sires, S; dams, D; sires and dams, S+D). Accordingly, 27 different selection schemes were included in the comparison of selection schemes: S_{WH}, S_{vWH}, S_{WH+vWH}, D_{WH}, D_{vWH}, D_{WH+vWH}, and $S+D_{WH}$, $S+D_{vWH}$, $S+D_{WH+vWH}$; S_{BMI}, S_{vBMI}, $S_{BMI+vBMI}$, D_{BMI}, D_{vBMI}, $D_{BMI+vBMI}$, and $S+D_{BMI}$, $S+D_{vBMI}$, $S+D_{BMI+vBMI}$; S_{WH+BMI}, $S_{vWH+vBMI}$, $S_{WH+BMI+vWH+vBMI}$, D_{WH+BMI}, $D_{vWH+vBMI}$, $D_{WH+BMI+vWH+vBMI}$, and $S+D_{WH+BMI}$, $S+D_{vWH+vBMI}$, $S+D_{WH+BMI+vWH+vBMI}$.

Results

Estimates of heritabilities and additive genetic correlations from the two bivariate analyses are given in Table 2. Moderate heritabilities, ranging between 0.19 and 0.41, were estimated for all traits. Concerning the relation between heritability estimates for the body measurements and their within litter variances, heritability of WH was 1.2 times larger than heritability of vWH, whilst heritability of BMI was only two-thirds of the heritability of vBMI. A negative additive genetic correlation of -0.11 was estimated between WH and vWH, and a positive additive genetic correlation of 0.11 was estimated between BMI and vBMI. Standard errors were < 0.02 for the heritabilities and < 0.03 for the additive genetic correlations.

Pearson correlation coefficients calculated between RBV for WH, vWH, BMI and vBMI in the parents of informants are given in Table 3. RBV correlations between body measurements and their within litter variances reflected the additive genetic correlations in both, sires and dams as well as in the parents of all dogs with conformation data and the dogs with at least one conformation evaluated litter mate. In the dams, negative correlations between RBV for WH and vWH were more distinct (r = -0.28 to -0.26) than in the sires (r = -0.18), but positive correlations between RBV for BMI and vBMI were very similar in sires and dams (r = 0.12 to 0.13). There was a consistent and significant negative correlation between RBV for WH and BMI (r = -0.20 to -0.16), whilst RBV for vBMI were largely uncorrelated with RBV for both WH and vWH (r = 0.00 to 0.06).

Proportions of phenotypic variance explained by own and parental RBV are given in Table 4. Concerning WH, analyses for both sexes together revealed considerably lower coefficients of determination than analyses performed separately for males and females. In the later, own RBV for WH explained 66 to 72% of WH variance, whereas corresponding sire RBV explained 19 to 20% and corresponding dam RBV explained 26 to 29% of WH variance. Differences between analyses for both sexes together and separate analyses in males and females were smaller for BMI than for WH. However, the proportions of phenotypic variance of BMI explained by respective RBV were generally lower. In the sex-specific analyses they ranged between 47 and 52% for own RBV, between 7 and 10% for sire RBV and between 15 and 17% for dam RBV. Proportions of phenotypic variance of WH and BMI explained by respective own or parental RBV were mostly higher in females than in males. Parental RBV for vWH and vBMI poorly explained vWH and vBMI in their offspring. However, coefficients of determination for own RBV were 0.12 for vWH and 0.37 for vBMI.

Tables 5 to 8 provide illustrations of the dependences of offspring phenotypes on the parental RBV. For males and females, distributions of WH, BMI and CHD phenotypes are given by the RBV of their sires and dams for WH (Tables 5 and 6) and BMI (Tables 7 and 8). Parental RBV for WH were in good agreement with WH distributions in male and female offspring. Mean WH of offspring increased with increasing sire and dam RBV for WH. Increase of mean WH on the diagonal, i.e. from the combination of lowest sire and dam RBV for WH to the highest combination of sire and dam RBV for WH, amounted to 3.8% in male dogs and 4.3% in female dogs. At the same time, there was little change in BMI distributions, with means on the diagonal changing by less than 2% (+0.8% in males, -1.5% in females). Corresponding behavior was seen with regard to BMI. Here, increase of mean BMI on the diagonal was 15.3% in the male dogs and 18.9% in the female dogs. There was no obvious pattern of WH distributions in the offspring in dependence on sire and dam RBV for BMI, with mean WH on the diagonal changing by less than 1%

(+0.3% in males, -0.5% in females). Dependency of CHD score on parental RBV for WH and BMI was less clear than for respective body measures themselves. However, mean CHD score was by 6.9% larger in males and by 2.2% larger in females in the offspring of sires and dams with highest RBV for WH when compared to offspring of sires and dams with lowest RBV for WH. Conversely, comparison of offspring of parents with highest and lowest RBV for BMI revealed a decrease of mean CHD scores by 14.6% in the males and 4.3% in the females.

Distributions of WH, BMI and CHD differed little and without clear pattern between combinations of sire and dam RBV for vWH and vBMI (Supplementary tables 1 to 4). Lowest standard deviations of WH and BMI were not seen in the offspring of parents with lowest RBV for vWH and vBMI, but matings of parents with lowest RBV for vWH resulted in lowest WH variation and matings of parents with lowest RBV for vBMI resulted in lowest BMI variation in male and female offspring.

Expected responses to selection in males and females under the selection scenarios studied are shown in Tables 9 to 11. Maximum decrease of mean WH was < 1% and maximum decrease of mean BMI was < 2% in both sexes and across selection scenarios. In each case, selection of sires and dams (S+D) increased the expected selection responses for mean WH and mean BMI by a factor of 1.6 to 3.3 over selection of only one parent (S or D). Selection for reduced WH was most efficient in decreasing mean WH, but standard deviations of WH tended to increase in both sexes under selection scenarios S_{WH}, D_{WH} and $S+D_{WH}$ (change from 0.89 to 0.91-0.96 in males and from 0.94 to 0.94-1.00 in females). Occurrence of excessive WH was not avoided by any of the compared selection scenarios, resulting in unchanged maximum WH in males (66.0 cm) and unchanged or slightly reduced maximum WH in females (61.0-61.5 cm). Conversely, use of RBV for BMI or vBMI for selection resulted in consistent decrease of BMI standard deviations (from 6.38 to 5.92-6.31 in males and from 6.48 to 5.84-6.40 in females) and maximum BMI under selection scenarios S_{BMI}, D_{BMI} and $S+D_{BMI}$. Under selection of sires and dams, the proportions of offspring of selected parents when compared to the offspring of all parents were in most cases in the order of 58-81%. However, joint consideration of RBV for WH and BMI resulted in a decrease of the proportions of offspring of selected parents to 30-43%. Side effects of selection for reduced WH, vWH, BMI or vBMI or combinations of these traits on CHD were mostly negligible. However, there was some increase of mean CHD scores of offspring when all parental RBV for all four traits had to be smaller than 120 (selection scenarios $S_{WH+BMI+vWH+vBMI}$, $D_{WH+BMI+vWH+vBMI}$, and $S+D_{WH+BMI+vWH+vBMI}$). This increase was small in females, but more distinct in males.

Discussion

Information on body measurements of GSD were used to investigate the opportunities for conformation selection in this dogs breed. Available data referred to male and female dogs which had been positively evaluated at breeding approvals of the SV in a time period of 12 years. Because of respective conformation requirements defined in the SV breeding standard, variation of WH and BW was rather limited in these data. The currently applied regulations for breeding approvals, having come into effect in 2007, limit the tolerable over- or undersize to 1 cm of WH. In our data, WH distribution in the males already fit this regulation, and WH range in the females was only slightly larger (maximum oversize of 1.5 cm). Size variation in the whole population of GSD is likely to be considerably larger, but conformation evaluation is routinely done only in the breeding candidates. Data on total distributions of conformation traits in the GSD are not available. However, heritabilities in the order of 0.4 document the still relevant additive genetic variance within the sample of conformation evaluated dogs, justifying its use as basis of genetic evaluation for conformation.

Within litter variances of body measurements were defined as separate traits to be considered for genetic evaluation. Previous studies on within litter variances of conformation, which were performed for pigs, used birth weight or weight at three weeks of age as reference (Damgaard et al. 2003, Wolf et al. 2008). Information on birth weight or weight at few weeks of age was not available for GSD, so definitions of within litter variances of conformation traits were again based on the data from breeding approvals at usually two years of age. Because calculation of within litter variance required two or more litter mates that had been approved as breeding animals, the problem of lacking population-wide conformation data was increased for this trait. However, regardless of the number of informative litters decreasing to less than one third, WH and BMI distributions in all dogs with conformation data and in dogs from litters with at least two dogs with conformation information were very similar. It was therefore concluded that dogs from litters with more than one approved dog were at least representative for all approved dogs. In the model used for the genetic analyses, dependence on proportions of approved dogs per litter and proportions of males among the approved litter mates was accounted for by respective class variables. Studies on birth weight of piglets have shown that within litter variance can be analyzed across sexes and is then adequately modeled by weighting for the proportion of males in the litter (Wittenburg et al. 2008). Because conformation data on whole litters was usually not available for the GSD, additional modeling of the amount of available information per litter was required. Nevertheless, the average proportion of approved dogs per litter was 46% in the dataset used for definition of within litter variances, and based on the available data, it was not possible to assess whether or to which extent the calculated variances among the approved dogs actually reflected within litter variances as they may have been calculated on the basis of population-wide conformation data.

In the studies on weight and weight variance of piglets, birth weight of individual piglets or of whole litters showed about 3- to 5-fold higher heritability than standard deviation or squared standard deviation, i.e. variance, of birth weight within litter (0.39 vs. 0.08, Damgaard et al. 2003; 0.13 vs. 0.04, Wolf et al. 2008). Additive genetic correlations in the order of 0.2 to 0.3 were estimated between the two traits. Although heritabilities of weight and its standard deviation within litter decreased with age, the positive additive genetic correlation was confirmed (Damgaard et al. 2003). In the GSD, use of adult conformation measurements made is necessary to account for WH differences when analyzing BW information. Accordingly, BMI, i.e. BW adjusted for WH, was considered, because it should better reflect the body proportions and the stature of the dog than BW alone. For BMI in the GSD, the relation between heritability of the conformation trait and heritability of its within litter variance was inverted when compared to the studies on porcine birth weight, but the additive genetic correlations between the BW related traits were similar. This similarity may be explained by the much larger impact of BW than WH on BMI which is due to consideration of BW in kg (in the numerator) and WH in m (in the denominator).

Allowed WH ranges for breeding animals limit WH variation within sex to maximally 0.07 m, whilst ranges of suggested BW are 10 kg in males and 8 kg in females. Furthermore, over- or underweight will hardly ever cause rejection of breeding candidates, so observed BW ranges were more than twice as large than the recommended ones (22.0kg in males, 21.5 kg in females).

Heritability estimates of 0.3 to 0.5 have been reported for WH in different breeds of dogs (Helmink et al. 2001, Dammann et al. 2009a, b), and our results were in agreement with these figures. vWH has not yet been included in population genetic studies in the dog. Furthermore, information on vWH is also missing in the studies on growth parameters in pigs, because neonatal or juvenile size measurement is rather uncommon in this species. For the GSD, we found a negative additive genetic correlation of -0.11 between WH and vWH, indicating that the necessary selection for smaller WH may lead to some increase of vWH as long as vWH remains unconsidered. Study of expected selection responses allowed quantification of the correlated selection responses in case of single trait selection on for example WH and comparison of efficiencies of single and multiple trait selection. Exclusion of parents with RBV > 120 meant low selection intensity, with between 75 and 80% of sires and dams fulfilling the selection criteria (results not shown). However, given the total spectrum of traits which may be relevant for selection in the GSD, including behavior and performance, more intense selection for conformation was considered unrealistic. Under the studied conditions, changes of distributions of conformation traits were mostly small, but illustrated the effects of selection on traits of different heritability in presence of genetic correlations of opposite sign. The breeding standard puts most weight on WH, so reduction of WH or at least avoidance of further increase of mean WH should be of primary interest. Instead of selecting on the basis of RBV for WH alone, simultaneous consideration of RBV for vWH will counteract decrease of litter homogeneity with respect to WH. Selection for smaller BMI and smaller vBMI may be suggested in view of the huge maxima and variations of BW and BMI in the approved dogs. However, unless selection is also for reduced WH, selection for reduced BMI will tend to worsen the problem of increasing mean WH. According to the results of this study, RBV based selection for conformation in the GSD may preferably include WH and vWH. Stability or slight improvement of mean CHD scores implied compatibility with the currently practiced breeding strategies that aim at reducing the number of GSD affected by CHD. Additional inclusion of RBV for BMI and vBMI in the selection conditions with regard to conformation resulted in a considerable reduction of the number of selected offspring, i.e. offspring from matings with one or both parents fulfilling the selection conditions. The negative additive genetic correlations between the traits take effect here. Furthermore, in the later case of multiple trait conformation selection there were indications for interference with selection against CHD. Use of RBV for WH and vWH for conformation selection is therefore recommended to maximize breeding success with regard to conformation and conformational homogeneity in the GSD.

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Tab. 1. Distribution of dogs with records for withers height (WH) and body mass index (BMI) and of WH, BMI, within litter variances of WH (vWH) and BMI (vBMI), and scores of canine hip dysplasia (CHD) in 36,028 German shepherd dogs from birth years 1992-2003.

Trait	All litters			Litters with at least two dogs with WH and BMI records		
	n	Mean ± SD	(Min-Max)	n	Mean ± SD	(Min-Max)
Litters						
n_{total}	26,155	1.38 ± 0.70	(1-7)	7,282	2.36 ± 0.67	(2-7)
n_{male}	26,155	0.55 ± 0.65	(0-5)	7,282	0.98 ± 0.81	(0-5)
n_{female}	26,155	0.83 ± 0.69	(0-5)	7,282	1.38 ± 0.82	(0-5)
p_{male}	26,155	0.39 ± 0.45	(0-1)	7,282	0.41 ± 0.32	(0-1)
Males (breeding standard: WH 60-65cm ⊥ 1cm, body weight 30-40 kg)						
WH	14,416	64.37 ± 0.89	(59.0-66.0)	7,136	64.36 ± 0.89	(59.5-66.0)
vWH				7,136	8.50 ± 6.60	(0.0-40.5)
BMI	14,416	88.00 ± 6.38	(61.0-114.7)	7,136	88.25 ± 6.33	(66.3-114.7)
vBMI				7,136	40.32 ± 51.62	(0.0-728.9)
CHD	12,289	1.38 ± 0.61	(1-4)	6,587	1.35 ± 0.60	(1-3)
Females (breeding standard: WH 55-60cm ⊥ 1cm, body weight 22-30 kg)						
WH	21,612	59.22 ± 0.94	(54.0-61.5)	10,018	59.22 ± 0.93	(54.0-61.5)
vWH				10,018	6.39 ± 6.60	(0.0-40.5)
BMI	21,612	82.75 ± 6.48	(58.3-120.0)	10,018	82.84 ± 6.46	(58.3-120.0)
vBMI				10,018	37.67 ± 50.38	(0.0-728.9)
CHD	19,115	1.37 ± 0.62	(1-4)	9,328	1.35 ± 0.61	(1-4)

n_{total} = total of number of dogs with WH and BMI records per litter; n_{male} (n_{female}) = number of male (female) dogs with WH and BMI records per litter; p_{male} = proportion of male dogs with WH and BMI records within litter

Tab. 2. Heritabilities and additive genetic correlations with their standard errors from bivariate analyses for the body measurements withers height (WH) and body mass index (BMI) and their within litter variances in the German shepherd dog.

Genetic parameter	WH	BMI
Heritabilities		
Body measurement	0.413 ⊥ 0.015	0.191 ⊥ 0.013
Within litter variance of the body measurement	0.331 ǀ 0.008	0.285 ǀ 0.008
Additive genetic correlation between body measurement and within litter variance of the body measurement	-0.111 + 0.016	0.111 + 0.024

Tab. 3 Correlations between breeding values for withers height (WH), body mass index (BMI) and their variances within litters (vWH, vBMI) in the parents of dogs with conformation data.

Trait	All litters			Litters with at least two dogs with WH and BMI records		
	vWH	BMI	vBMI	vWH	BMI	vBMI
Sires ($n_{S\ all}$ = 5,427; $n_{S\ var}$ = 2,001)						
WH	-0.179	-0.192	-0.055	-0.176	-0.197	-0.034
vWH		0.001	0.014		0.008	0.012
BMI			0.132			0.118
Dams ($n_{D\ all}$ = 15,439; $n_{D\ var}$ = 5,436)						
WH	-0.278	-0.168	-0.052	-0.261	-0.155	-0.041
vWH		0.009	0.045		-0.003	0.059
BMI			0.130			0.133

$n_{S\ all}$ ($n_{D\ all}$) = number of sires (dams) of all 36,028 dogs with conformation data; $n_{S\ var}$ ($n_{D\ var}$) = number of sires (dams) of the 17,154 dogs with conformation data from litters with at least two conformation evaluated litter mates

Tab. 4. Proportions of phenotypic variance of withers height (WH) and body mass index (BMI) and their within litter variances (vWH, vBMI) explained by respective breeding values predicted for the individual dog (RBV_{ind}) or its sire (RBV_{sire}) or dam (RBV_{dam}) in 36,028 German shepherd dogs with information on WH and BMI.

Trait	All litters			Litters with at least two dogs with WH and BMI records		
	males + females (n=36,028)	males (n=14,416)	females (n=21,612)	males + females (n=17,154)	males (n=7,136)	females (n=10,018)
WH						
RBV_{ind}	0.202	0.695	0.720	0.178	0.663	0.702
RBV_{sire}	0.175	0.202	0.202	0.136	0.186	0.195
RBV_{dam}	0.145	0.280	0.288	0.129	0.258	0.274
vWH						
RBV_{ind}				0.119		
RBV_{sire}				0.018		
RBV_{dam}				0.024		
BMI						
RBV_{ind}	0.452	0.495	0.518	0.429	0.470	0.490
RBV_{sire}	0.084	0.079	0.099	0.085	0.074	0.102
RBV_{dam}	0.153	0.154	0.172	0.142	0.153	0.158
vBMI						
RBV_{ind}				0.369		
RBV_{sire}				0.053		
RBV_{dam}				0.074		

Tab. 5. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for WH of their parents ($RBV_{WH\ sire}$, $RBV_{WH\ dam}$), considering 14,416 male dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{WH\ sire}$	$RBV_{WH\ dam}$				
	< 60 (n_d=383)	60-79 (n_d=965)	80-99 (n_d=2,674)	100-119 (n_d=3,675)	≥ 120 (n_d=1,443)
< 60 (n_s=203)	**n=161** **62.57 ± 1.28** **(60.0-65.0)** **87.96 ± 7.05** **(74.2-112.1)** **1.30 ± 0.59** **(1-3)**	n=248 63.12 ± 1.12 (60.0-65.0) 87.9 ± 6.76 (71.8-112.3) 1.34 ± 0.60 (1-3)	n=279 63.56 ± 0.96 (60.0-66.0) 88.69 ± 6.28 (68.4-112.8) 1.31 ± 0.58 (1-3)	n=191 64.12 ± 0.85 (62.0-66.0) 89.92 ± 6.59 (72.1-108.9) 1.30 ± 0.58 (1-3)	n=42 64.56 ± 0.85 (62.5-66.0) 90.15 ± 6.55 (78.1-106.5) 1.33 ± 0.53 (1-3)
60-79 (n_s=448)	n=200 63.02 ± 1.26 (59.0-65.0) 88.00 ± 7.17 (67.0-108.3) 1.27 ± 0.53 (1-3)	**n=443** **63.42 ± 1.07** **(60.0-66.0)** **88.87 ± 6.74** **(61.0-109.3)** **1.33 ± 0.61** **(1-3)**	n=603 63.83 ± 0.91 (60.0-66.0) 89.11 ± 7.04 (69.7-114.7) 1.30 ± 0.56 (1-3)	n=303 64.42 ± 0.76 (62.0-66.0) 89.35 ± 6.54 (71.0-108.9) 1.28 ± 0.52 (1-3)	n=65 64.78 ± 0.54 (63.0-66.0) 89.06 ± 6.47 (73.4-104.1) 1.35 ± 0.54 (1-3)
80-99 (n_s=936)	n=247 63.36 ± 1.12 (60.0-65.5) 88.63 ± 6.64 (69.9-110.6) 1.31 + 0.60 (1-3)	n=503 63.78 ± 1.01 (59.5-66.0) 88.79 ± 6.72 (68.4-108.3) 1.33 + 0.59 (1-3)	**n=1,057** **64.15 ± 0.77** **(62.0-66.0)** **88.11 ± 6.55** **(67.0-112.3)** **1.33 ± 0.58** **(1-3)**	n=849 64.51 ± 0.69 (61.0-66.0) 88.22 ± 6.37 (66.1-109.9) 1.43 + 0.66 (1-3)	n=210 64.84 ± 0.57 (62.0-66.0) 89.19 ± 6.39 (74.6-108.2) 1.28 + 0.52 (1-3)
100-119 (n_s=1,296)	n=104 63.80 ± 0.96 (61.5-66.0) 89.01 + 6.70 (73.3-106.5) 1.36 + 0.61 (1-3)	n=315 63.98 ± 0.95 (60.0-66.0) 87.70 + 6.55 (67.0-108.9) 1.31 + 0.56 (1-3)	n=1,241 64.33 ± 0.71 (61.0-66.0) 87.24 + 6.29 (61.5-106.5) 1.46 + 0.66 (1-3)	**n=2,387** **64.64 ± 0.60** **(61.0-66.0)** **87.25 ± 6.20** **(66.3-107.7)** **1.41 ± 0.64** **(1-4)**	n=1,078 64.84 ± 0.43 (62.5-66.0) 87.70 + 6.22 (68.6-107.2) 1.46 + 0.66 (1-3)
≥ 120 (n_s=626)	n=27 64.06 + 0.92 (62.0-65.0) 88.13 + 6.19 (75.7-104.1) 1.22 + 0.58 (1-3)	n=108 64.26 + 0.81 (61.5-66.0) 86.82 + 6.24 (70.5-110.9) 1.39 + 0.61 (1-3)	n=816 64.55 + 0.65 (61.0-66.0) 87.26 + 6.10 (66.3-107.7) 1.38 + 0.59 (1-3)	n=1,992 64.77 + 0.52 (60.0-66.0) 87.97 + 6.04 (66.3-108.3) 1.38 + 0.60 (1-3)	**n=947** **64.93 ± 0.37** **(63.0-66.0)** **88.66 ± 5.88** **(66.3-106.5)** **1.39 ± 0.62** **(1-3)**

Tab. 6. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for WH of their parents ($RBV_{WH\ sire}$, $RBV_{WH\ dam}$), considering 21,612 female dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{WH\ sire}$			$RBV_{WH\ dam}$		
	< 60 (n_d=469)	60-79 (n_d=1,186)	80-99 (n_d=3,335)	100-119 (n_d=4,849)	≥ 120 (n_d=1,998)
< 60 (n_s=220)	**n=210** **57.38 ± 1.16** **(55.0-61.0)** **84.34 ± 7.50** **(66.5-113.0)** **1.36 ± 0.61** **(1-3)**	n=308 57.80 + 1.16 (54.0-61.0) 84.67 ⊥ 6.81 (67.2-110.0) 1.31 ⊥ 0.59 (1-3)	n=340 58.32 + 1.02 (55.0-61.0) 85.21 ⊥ 6.66 (61.4-120.0) 1.27 ⊥ 0.52 (1-3)	n=204 58.84 + 0.93 (56.0-61.0) 86.21 ⊥ 6.66 (70.6-107.0) 1.24 ⊥ 0.55 (1-3)	n=68 59.26 + 0.91 (57.0-61.0) 84.39 ⊥ 6.74 (69.4-98.6) 1.34 ⊥ 0.62 (1-3)
60-79 (n_s=491)	n=252 57.91 ⊥ 1.14 (55.0-61.0) 83.56 ⊥ 6.95 (61.6-115.4) 1.35 ⊥ 0.60 (1-3)	**n=535** **58.17 ± 1.11** **(55.0-61.0)** **84.25 ± 6.80** **(63.9-115.9)** **1.30 ± 0.58** **(1-3)**	n=736 58.63 ⊥ 0.96 (55.0-61.0) 84.47 ⊥ 6.66 (62.4-114.3) 1.27 ⊥ 0.55 (1-3)	n=402 59.15 ⊥ 0.88 (56.0-61.0) 84.45 ⊥ 6.69 (62.1-109.2) 1.33 ⊥ 0.58 (1-3)	n=69 59.55 ⊥ 0.69 (57.5-61.0) 85.33 ⊥ 7.46 (72.2-105.6) 1.36 ⊥ 0.67 (1-4)
80-99 (n_s=1,099)	n=340 58.15 ⊥ 1.01 (55.0-60.0) 84.05 ⊥ 5.98 (66.2-100.5) 1.39 ⊥ 0.65 (1-3)	n=684 58.46 ⊥ 1.01 (55.0-61.0) 84.29 ⊥ 6.90 (65.4-118.0) 1.35 ⊥ 0.60 (1-4)	**n=1,372** **58.87 ± 0.87** **(55.0-61.0)** **83.45 ± 6.86** **(60.9-112.0)** **1.35 ± 0.59** **(1-3)**	n=1,217 59.27 ⊥ 0.58 (57.5-61.0) 82.89 ⊥ 6.81 (61.1-111.6) 1.39 ⊥ 0.64 (1-3)	n=384 59.68 ⊥ 0.58 (57.5-61.0) 82.97 ⊥ 6.84 (58.3-112.0) 1.38 ⊥ 0.64 (1-3)
100-119 (n_s=1,635)	n=119 58.58 ⊥ 1.12 (56.0-61.0) 83.90 ⊥ 6.61 (64.6-107.7) 1.27 + 0.54 (1-3)	n=441 58.67 ⊥ 1.01 (55.0-61.0) 83.10 ⊥ 6.97 (63.9-111.0) 1.35 + 0.62 (1-3)	n=1,860 59.04 ⊥ 0.82 (55.0-61.0) 81.69 ⊥ 6.41 (62.4-116.4) 1.40 + 0.64 (1-3)	**n=3,760** **59.46 ± 0.69** **(56.0-61.0)** **81.84 ± 6.19** **(58.3-115.3)** **1.38 ± 0.62** **(1-4)**	n=1,876 59.71 ⊥ 0.52 (57.0-61.0) 81.91 ⊥ 6.00 (61.1-108.3) 1.39 + 0.62 (1-4)
≥ 120 (n_s=791)	n=42 58.63 ⊥ 1.02 (56.5-61.0) 84.23 + 7.53 (71.8-107.0) 1.17 + 0.38 (1-2)	n=177 58.88 ⊥ 1.00 (56.0-61.0) 81.85 + 6.57 (66.7-107.7) 1.45 + 0.63 (1-3)	n=1,247 59.33 ⊥ 0.75 (56.0-61.0) 81.95 + 6.57 (58.4-108.9) 1.38 + 0.65 (1-4)	n=3,259 59.64 ⊥ 0.58 (56.5-61.5) 82.39 + 6.06 (60.3-112.0) 1.39 + 0.63 (1-3)	**n=1,710** **59.87 ± 0.41** **(57.0-61.5)** **83.05 ± 5.89** **(58.3-108.3)** **1.39 ± 0.63** **(1-3)**

Tab. 7. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for BMI of their parents ($RBV_{BMI\ sire}$, $RBV_{BMI\ dam}$), considering 14,416 male dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{BMI\ sire}$	$RBV_{BMI\ dam}$ < 60 (n_d=177)	 60-79 (n_d=1,121)	 80-99 (n_d=3,294)	 100-119 (n_d=3,167)	 ≥ 120 (n_d=1,381)
< 60 (n_s=82)	**n=23** **63.98 ± 0.71** **(63.0-65.0)** **80.88 ± 5.50** **(71.0-91.8)** **1.58 ± 0.69** **(1-3)**	n=157 64.49 + 0.70 (62.0-66.0) 83.11 ⊥ 5.47 (70.8-99.4) 1.45 ⊥ 0.69 (1-3)	n=363 64.56 + 0.70 (61.0-66.0) 84.70 ⊥ 5.41 (68.6-99.4) 1.39 ⊥ 0.63 (1-3)	n=222 64.65 + 0.65 (61.0-66.0) 86.79 ⊥ 5.93 (69.4-99.4) 1.45 ⊥ 0.61 (1-3)	n=59 64.64 + 0.54 (63.0-65.0) 88.65 ⊥ 5.55 (78.1-106.5) 1.49 ⊥ 0.67 (1-3)
60-79 (n_s=398)	n=51 64.44 ⊥ 0.64 (62.5-65.0) 81.38 ⊥ 5.87 (67.0-92.8) 1.42 ⊥ 0.66 (1-3)	**n=362** **64.41 ± 0.80** **(60.0-66.0)** **83.05 ± 5.59** **(66.3-98.6)** **1.39 ± 0.59** **(1-3)**	n=860 64.35 ⊥ 0.85 (60.0-66.0) 84.70 ⊥ 5.56 (66.3-101.8) 1.40 ⊥ 0.63 (1-3)	n=742 64.44 ⊥ 0.83 (60.0-66.0) 87.83 ⊥ 5.61 (61.5-107.4) 1.39 ⊥ 0.64 (1-3)	n=271 64.26 ⊥ 0.90 (61.0-66.0) 89.28 ⊥ 6.10 (70.5-107.1) 1.42 ⊥ 0.65 (1-3)
80-99 (n_s=1,166)	n=87 64.48 ⊥ 0.68 (63.0-66.0) 83.28 ⊥ 5.30 (73.2-95.2) 1.37 ⊥ 0.62 (1-3)	n=495 64.44 ⊥ 0.83 (60.0-66.0) 83.64 ⊥ 5.72 (66.3-108.3) 1.47 ⊥ 0.65 (1-3)	**n=1,495** **64.45 ± 0.81** **(60.0-66.0)** **85.45 ± 5.67** **(66.1-103.3)** **1.41 ± 0.63** **(1-3)**	n=1,216 64.45 ⊥ 0.85 (60.0-66.0) 88.95 ⊥ 5.55 (69.1-106.5) 1.39 ⊥ 0.64 (1-3)	n=412 64.20 ⊥ 1.04 (60.0-66.0) 90.54 ⊥ 6.14 (70.2-107.7) 1.32 ⊥ 0.58 (1-3)
100-119 (n_s=1,225)	n=104 64.51 ⊥ 0.63 (62.0-65.5) 84.40 ⊥ 4.56 (73.2-94.9) 1.36 + 0.57 (1-3)	n=496 64.44 ⊥ 0.85 (59.5-66.0) 85.28 ⊥ 5.99 (61.0-106.5) 1.33 + 0.58 (1-3)	n=1,431 64.44 ⊥ 0.85 (59.5-66.0) 87.46 ⊥ 5.43 (69.4-107.2) 1.37 + 0.61 (1-4)	**n=1,578** **64.39 ± 0.89** **(60.5-66.0)** **89.84 ± 5.54** **(71.0-106.5)** **1.35 ± 0.59** **(1-3)**	n=746 64.17 ⊥ 1.09 (59.0-66.0) 91.22 ⊥ 6.39 (69.4-110.4) 1.31 + 0.58 (1-3)
≥ 120 (n_s=638)	n=42 64.42 ⊥ 0.97 (60.0-66.0) 84.84 + 5.18 (73.2-94.7) 1.39 + 0.59 (1-3)	n=272 64.40 ⊥ 0.86 (60.0-66.0) 86.84 + 5.91 (68.0-101.8) 1.40 + 0.63 (1-3)	n=839 64.31 ⊥ 0.88 (61.0-66.0) 88.69 + 5.86 (70.8-109.9) 1.33 + 0.58 (1-3)	n=1,124 64.22 ⊥ 0.98 (60.0-66.0) 90.97 + 5.66 (71.0-110.6) 1.40 + 0.62 (1-3)	**n=969** **64.14 ± 1.02** **(60.0-66.0)** **93.22 ± 6.51** **(72.0-114.7)** **1.35 ± 0.60** **(1-3)**

Tab. 8. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for BMI of their parents ($RBV_{BMI\ sire}$, $RBV_{BMI\ dam}$), considering 21,612 female dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{BMI\ sire}$			$RBV_{BMI\ dam}$		
	< 60 (n_d=254)	60-79 (n_d=1,452)	80-99 (n_d=4,445)	100-119 (n_d=3,959)	≥ 120 (n_d=1,727)
< 60 (n_s=112)	**n=55** **59.18 ± 0.68** **(57.5-60.0)** **74.83 ± 5.45** **(63.2-87.66)** **1.40 ± 0.65** **(1-3)**	n=225 59.27 + 0.85 (56.0-60.0) 76.68 ⊥ 5.35 (62.4-90.3) 1.41 ⊥ 0.60 (1-3)	n=584 59.35 + 0.76 (56.0-61.0) 78.62 ⊥ 5.27 (61.1-94.4) 1.43 ⊥ 0.64 (1-3)	n=369 59.37 + 0.80 (56.0-61.0) 81.46 ⊥ 5.56 (58.3-100.5) 1.44 ⊥ 0.66 (1-3)	n=98 59.34 + 0.74 (57.5-60.0) 83.31 ⊥ 6.31 (72.2-111.0) 1.39 ⊥ 0.62 (1-3)
60-79 (n_s=521)	n=93 59.25 ⊥ 0.74 (57.0-60.0) 75.99 ⊥ 5.30 (63.2-88.9) 1.53 ⊥ 0.75 (1-3)	**n=588** **59.27 ± 0.84** **(56.0-61.0)** **77.73 ± 5.27** **(60.9-94.4)** **1.40 ± 0.63** **(1-3)**	n=1,473 59.25 ⊥ 0.85 (55.0-61.0) 80.06 ⊥ 5.45 (59.3-106.3) 1.39 ⊥ 0.63 (1-3)	n=1,144 59.26 ⊥ 0.85 (56.0-61.0) 82.81 ⊥ 5.82 (64.3-108.3) 1.37 ⊥ 0.62 (1-3)	n=364 59.19 ⊥ 0.95 (56.0-61.0) 84.42 ⊥ 6.53 (66.1-109.2) 1.38 ⊥ 0.65 (1-3)
80-99 (n_s=1,448)	n=173 59.36 ⊥ 0.81 (56.0-60.5) 77.52 ⊥ 5.37 (63.2-97.2) 1.44 ⊥ 0.65 (1-3)	n=808 59.36 ⊥ 0.79 (56.0-61.0) 79.00 ⊥ 5.26 (58.4-94.8) 1.42 ⊥ 0.64 (1-3)	**n=2,383** **59.27 ± 0.88** **(55.0-61.0)** **80.64 ± 5.34** **(62.4-104.0)** **1.38 ± 0.64** **(1-3)**	n=1,765 59.27 ⊥ 0.91 (55.5-61.5) 83.19 ⊥ 5.51 (62.4-116.4) 1.37 ⊥ 0.61 (1-3)	n=585 59.12 ⊥ 1.00 (55.0-61.0) 85.12 ⊥ 6.19 (69.4-115.3) 1.34 ⊥ 0.61 (1-4)
100-119 (n_s=1,400)	n=148 59.33 ⊥ 0.83 (57.0-61.0) 78.22 ⊥ 5.55 (63.2-89.3) 1.29 + 0.53 (1-3)	n=723 59.33 ⊥ 0.81 (56.0-60.5) 80.19 ⊥ 5.50 (58.3-99.3) 1.35 + 0.61 (1-3)	n=2,175 59.28 ⊥ 0.92 (54.0-61.0) 82.10 ⊥ 5.46 (63.9-109.2) 1.38 + 0.62 (1-3)	**n=2,197** **59.24 ± 0.99** **(55.0-61.0)** **84.75 ± 5.78** **(61.8-109.6)** **1.36 ± 0.61** **(1-4)**	n=1,026 59.05 ⊥ 1.11 (55.0-61.0) 87.15 ⊥ 6.55 (63.9-114.3) 1.31 + 0.58 (1-3)
≥ 120 (n_s=755)	n=80 59.48 ⊥ 0.77 (57.0-60.5) 79.46 + 5.69 (68.4-96.4) 1.30 + 0.65 (1-3)	n=427 59.28 ⊥ 0.91 (55.0-61.0) 81.33 + 5.51 (63.9-98.9) 1.37 + 0.59 (1-3)	n=1,261 59.19 ⊥ 0.98 (55.0-61.5) 83.37 + 5.67 (61.6-108.3) 1.40 + 0.63 (1-3)	n=1,515 59.09 ⊥ 1.00 (55.0-61.0) 86.06 + 6.18 (1.33 - 0.60) 1.33 + 0.60 (1-4)	**n=1,353** **58.91 ± 1.11** **(55.0-61.0)** **88.96 ± 6.96** **(65.0-120.0)** **1.34 ± 0.58** **(1-3)**

Tab. 9. Expected responses to selection with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line), when selection is performed for withers height (WH) or within litter variance of WH (vWH) or WH and vWH in sires (S) or dams (D) or sires and dams (S+D), in the German shepherd dog

Selection criterion	Males			Females		
	n	Mean ± SD	(Min-Max)	n	Mean ± SD	(Min-Max)
No selection						
	14,416	64.37 ± 0.89	(59.0-66.0)	21,612	59.22 ± 0.94	(54.0-61.5)
		88.00 ± 6.38	(61.0-114.7)		82.75 ± 6.48	(58.3-120.0)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
WH						
S	10,796	64.24 ± 0.94	(59.0-66.0)	15,649	59.07 ± 0.98	(54.0-61.0)
		88.01 ± 6.48	(61.0-114.7)		82.84 ± 6.60	(58.3-120.0)
		1.38 ± 0.62	(1-4)		1.36 ± 0.61	(1-4)
D	12,358	64.28 ± 0.91	(59.0-66.0)	17,977	59.11 ± 0.96	(54.0-61.5)
		87.93 ± 6.41	(61.0-114.7)		82.76 ± 6.55	(58.3-120.0)
		1.37 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
S+D	9,511	64.16 ± 0.96	(59.0-66.0)	13,410	58.96 ± 1.00	(54.0-61.0)
		87.98 ± 6.51	(61.0-114.7)		82.91 ± 6.65	(58.3-120.0)
		1.37 ± 0.62	(1-4)		1.36 ± 0.61	(1-4)
vWH						
S	12,966	64.39 ± 0.87	(59.0-66.0)	19,601	59.26 ± 0.91	(54.0-61.5)
		87.97 ± 6.37	(61.5-114.7)		82.71 ± 6.45	(58.3-120.0)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
D	13,254	64.38 ± 0.88	(59.0-66)	20,097	59.25 ± 0.91	(55.0-61.5)
		87.97 ± 6.33	(61.0-112.8)		82.70 ± 6.47	(58.3-120.0)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
S+D	11,976	64.40 ± 0.86	(59.0-66.0)	18,292	59.29 ± 0.89	(55.0-61.5)
		87.94 ± 6.32	(66.3-112.8)		82.66 ± 6.45	(58.3-120.0)
		1.39 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
WH and vWH						
S	9,453	64.25 ± 0.93	(59.0-66.0)	13,814	59.10 ± 0.96	(54.0-61.0)
		87.97 ± 6.48	(61.5-114.7)		82.78 ± 6.57	(58.3-120.0)
		1.39 ± 0.62	(1-4)		1.36 ± 0.62	(1-4)
D	11,243	64.29 ± 0.91	(59.0-66.0)	16,531	59.14 ± 0.94	(55.0-61.5)
		87.89 ± 6.36	(61.0-112.8)		82.71 ± 6.55	(58.3-120.0)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
S+D	7,496	64.18 ± 0.94	(59.0-66.0)	10,816	59.02 ± 0.97	(55.0-61.0)
		87.89 ± 6.45	(66.3-112.8)		82.80 ± 6.64	(58.3-120.0)
		1.39 ± 0.62	(1-4)		1.36 ± 0.62	(1-3)

Tab. 10. Expected responses to selection with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line), when selection is performed for body mass index (BMI) or within litter variance of BMI (vBMI) or BMI and vBMI in sires (S) or dams (D) or sires and dams (S+D), in the German shepherd dog.

Selection criterion	Males			Females		
	n	Mean ± SD	(Min-Max)	n	Mean ± SD	(Min-Max)
No selection						
	14,416	64.37 ± 0.89	(59.0-66.0)	21,612	59.22 ± 0.94	(54.0-61.5)
		88.00 ± 6.38	(61.0-114.7)		82.75 ± 6.48	(58.3-120.0)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
BMI						
S	11,375	64.41 ± 0.86	(59.0-66.0)	17,263	59.26 ± 0.91	(54.0-61.5)
		87.28 ± 6.18	(61.0-112.1)		82.00 ± 6.17	(58.3-116.4)
		1.38 ± 0.62	(1-4)		1.38 ± 0.62	(1-4)
D	12,073	64.40 ± 0.85	(59.5-66.0)	18,329	59.26 ± 0.90	(54.0-61.5)
		87.29 ± 6.10	(61.0-110.6)		81.96 ± 6.07	(58.3-116.4)
		1.39 ± 0.62	(1-4)		1.38 ± 0.62	(1-4)
S+D	9,948	64.44 ± 0.83	(59.5-66.0)	15,254	59.28 ± 0.88	(54.0-61.5)
		86.79 ± 6.01	(61.0-108.3)		81.48 ± 5.92	(58.3-116.4)
		1.39 ± 0.62	(1-4)		1.38 ± 0.63	(1-4)
vBMI						
S	12,687	64.38 ± 0.88	(59.5-66.0)	18,966	59.24 ± 0.93	(55.0-61.5)
		87.87 ± 6.31	(61.5-112.8)		82.70 ± 6.39	(58.3-116.4)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
D	13,203	64.38 ± 0.88	(59.0-66.0)	19,884	59.23 ± 0.93	(55.0-61.5)
		87.87 ± 6.28	(61.0-114.7)		82.71 ± 6.40	(58.3-120.0)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
S+D	11,672	64.39 ± 0.87	(59.5-66.0)	17,516	59.24 ± 0.92	(55.0-61.5)
		87.77 ± 6.24	(61.5-112.8)		82.67 ± 6.35	(59.3-115.4)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
BMI and vBMI						
S	10,273	64.41 ± 0.86	(59.5-66.0)	15,531	59.27 ± 0.90	(55.0-61.5)
		87.21 ± 6.14	(61.5-110.2)		82.01 ± 6.12	(58.3-116.4)
		1.38 ± 0.62	(1-4)		1.38 ± 0.62	(1-4)
D	11,258	64.41 ± 0.85	(59.5-66.0)	17,105	59.26 ± 0.90	(55.0-61.5)
		87.22 ± 6.04	(61.0-110.6)		81.96 ± 6.01	(58.3-115.4)
		1.39 ± 0.62	(1-4)		1.38 ± 0.62	(1-4)
S+D	8,426	64.44 ± 0.83	(59.5-66.0)	12,901	59.28 ± 0.88	(55.0-61.5)
		86.67 ± 5.92	(61.5-108.3)		81.51 ± 5.84	(59.3-109.6)
		1.39 ± 0.62	(1-4)		1.38 ± 0.63	(1-4)

Tab. 11. Expected responses to selection with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line), when selection is performed for withers height (WH) and body mass index (BMI) or within litter variances of WH (vWH) and BMI (vBMI) or WH, BMI, vWH and vBMI in sires (S) or dams (D) or sires and dams (S+D), in the German shepherd dog.

Selection criterion	Males			Females		
	n	Mean ± SD	(Min-Max)	n	Mean ± SD	(Min-Max)
No selection						
	14,416	64.37 ± 0.89	(59.0-66.0)	21,612	59.22 ± 0.94	(54.0-61.5)
		88.00 ± 6.38	(61.0-114.7)		82.75 ± 6.48	(58.3-120.0)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
WH and BMI						
S	8,485	64.30 ± 0.91	(59.0-66.0)	12,550	59.12 ± 0.95	(54.0-61.0)
		87.19 ± 6.24	(61.0-112.1)		81.97 ± 6.23	(58.3-116.4)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
D	10,323	64.32 ± 0.88	(59.5-66.0)	15,228	59.15 ± 0.93	(54.0-61.5)
		87.18 ± 6.10	(61.0-110.6)		81.93 ± 6.13	(58.3-116.4)
		1.38 ± 0.61	(1-4)		1.37 ± 0.62	(1-4)
S+D	6,279	64.24 ± 0.91	(59.5-66.0)	9,128	59.04 ± 0.96	(54.0-61.0)
		86.50 ± 6.02	(61.0-107.4)		81.35 ± 5.97	(58.3-116.4)
		1.39 ± 0.62	(1-4)		1.38 ± 0.63	(1-3)
vWH and vBMI						
S	11,466	64.40 ± 0.86	(59.5-66.0)	17,269	59.27 ± 0.90	(55.0-61.5)
		87.83 ± 6.31	(61.5-112.8)		82.65 ± 6.36	(58.3-116.4)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
D	12,215	64.39 ± 0.87	(59.0-66.0)	18,571	59.26 ± 0.91	(55.0-61.5)
		87.85 ± 6.25	(61.0-112.8)		82.67 ± 6.40	(58.3-120.0)
		1.38 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
S+D	9,839	64.42 ± 0.85	(59.5-66.0)	14,971	59.30 ± 0.88	(55.0-61.5)
		87.72 ± 6.20	(66.3-112.8)		82.60 ± 6.33	(59.3-115.3)
		1.39 ± 0.62	(1-4)		1.37 ± 0.62	(1-4)
WH, BMI, vWH and vBMI						
S	6,797	64.31 ± 0.90	(59.5-66.0)	10,037	59.17 ± 0.92	(55.0-61.0)
		87.07 ± 6.18	(61.5-112.1)		81.92 ± 6.16	(58.3-116.4)
		1.40 ± 0.63	(1-4)		1.37 ± 0.62	(1-4)
D	8,916	64.34 ± 0.87	(59.5-66.0)	13,311	59.18 ± 0.91	(55.0-61.5)
		87.11 ± 6.01	(61.0-110.6)		81.92 ± 6.07	(58.3-115.4)
		1.39 ± 0.62	(1-4)		1.38 ± 0.63	(1-3)
S+D	4,384	64.27 ± 0.88	(59.5-66.0)	6,444	59.09 ± 0.92	(55.0-61.0)
		86.36 ± 5.91	(66.3-106.5)		81.34 ± 5.89	(59.3-109.2)
		1.42 ± 0.63	(1-4)		1.39 ± 0.63	(1-3)

Suppl. Tab. 1. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for within litter variance of WH of their parents ($RBV_{vWH\ sire}$, $RBV_{vWH\ dam}$), considering 14,416 male dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{vWH\ sire}$	$RBV_{vWH\ dam}$			
	< 80 (n_d=618)	80-99 (n_d=3,433)	100-119 (n_d=4,381)	≥ 120 (n_d=708)
< 80 (n_s=394)	**n=235** **64.20 ± 0.96** **(60.0-66.0)** **89.13 ± 6.39** **(71.0-106.6)** **1.37 ± 0.61** **(1-3)**	n=995 64.34 + 0.86 (60.0-66.0) 88.29 + 6.21 (69.4-108.9) 1.37 ± 0.61 (1-3)	n=1,147 64.30 + 0.89 (60.0-66.0) 88.15 + 6.58 (67.0-112.3) 1.35 ± 0.60 (1-3)	n=291 64.07 + 0.98 (60.0-66.0) 88.45 + 6.64 (66.3-114.7) 1.30 ± 0.56 (1-3)
80-99 (n_s=1,267)	n=374 64.36 ± 0.95 (60.0-66.0) 88.15 ± 6.42 (68.4-105.0) 1.42 ± 0.63 (1-3)	**n=2,219** **64.46 ± 0.80** **(60.0-66.0)** **87.80 ± 6.23** **(66.3-110.1)** **1.39 ± 0.62** **(1-4)**	n=2,402 64.46 ± 0.82 (59.5-66.0) 87.79 ± 6.06 (68.4-112.3) 1.40 ± 0.61 (1-3)	n=388 64.27 ± 0.89 (60.0-66.0) 88.76 ± 7.20 (66.1-110.9) 1.38 ± 0.64 (1-3)
100-119 (n_s=1,452)	n=329 64.39 ± 0.87 (61.0-66.0) 88.48 ± 6.26 (71.0-112.8) 1.34 + 0.62 (1-3)	n=1,756 64.47 ± 0.84 (59.0-66.0) 87.83 ± 6.44 (67.0-110.4) 1.41 + 0.63 (1-3)	**n=2,289** **64.34 ± 0.91** **(60.0-66.0)** **87.79 ± 6.40** **(66.3-112.1)** **1.40 ± 0.64** **(1-3)**	n=341 64.31 ± 0.99 (60.0-66.0) 87.85 ± 6.83 (61.5-106.5) 1.34 + 0.60 (1-3)
≥ 120 (n_s=396)	n=174 64.19 + 0.93 (61.0-66.0) 89.33 + 6.35 (72.1-106.6) 1.20 ± 0.46 (1-3)	n=614 64.26 + 0.97 (60.0-66.0) 88.26 + 6.46 (68.6-106.7) 1.36 ± 0.60 (1-3)	n=653 64.21 + 1.06 (60.0-66.0) 88.04 + 6.57 (61.0-111.1) 1.35 ± 0.60 (1-3)	**n=209** **64.15 ± 1.04** **(59.5-66.0)** **88.30 ± 6.43** **(70.8-103.4)** **1.25 ± 0.52** **(1-3)**

Suppl. Tab. 2. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for within litter variance of WH of their parents ($RBV_{vWH\ sire}$, $RBV_{vWH\ dam}$), considering 21,612 female dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{vWH\ sire}$	$RBV_{vWH\ dam}$			
	< 80 (n_d=796)	80-99 (n_d=4,464)	100-119 (n_d=5,727)	≥ 120 (n_d=850)
< 80 (n_s=466)	**n=327** **59.30 ± 0.83** **(56.5-61.0)** **82.87 ± 6.26** **(68.1-102.8)** **1.32 ± 0.57** **(1-3)**	n=1,545 59.39 + 0.81 (55.0-61.0) 82.80 + 6.05 (63.9-105.6) 1.34 ⊥ 0.60 (1-4)	n=1,640 59.23 + 0.93 (55.0-61.5) 83.15 + 6.54 (61.1-120.0) 1.36 ⊥ 0.61 (1-3)	n=320 58.91 + 1.03 (56.0-61.0) 83.38 + 6.20 (68.6-104.0) 1.38 ⊥ 0.62 (1-4)
80-99 (n_s=1,546)	n=555 59.41 ı 0.88 (55.0-61.0) 83.13 ⊥ 6.71 (61.1-109.2) 1.32 ⊥ 0.62 (1-3)	**n=3,322** **59.44 ± 0.77** **(55.0-61.5)** **82.51 ± 6.51** **(58.3-115.3)** **1.37 ± 0.62** **(1-3)**	n=3,788 59.23 ı 0.90 (55.0-61.0) 82.57 ⊥ 6.38 (58.3-116.4) 1.39 ⊥ 0.62 (1-4)	n=556 58.95 ı 1.10 (55.0-61.0) 83.09 ⊥ 6.61 (62.4-104.8) 1.36 ⊥ 0.62 (1-4)
100-119 (n_s=1,786)	n=521 59.32 ⊥ 0.92 (56.5-61.0) 82.63 ⊥ 6.56 (63.9-108.3) 1.34 + 0.58 (1-3)	n=2,762 59.35 ⊥ 0.85 (55.0-61.0) 82.54 ⊥ 6.27 (63.9-112.0) 1.38 + 0.63 (1-3)	**n=3,476** **59.11 ± 0.99** **(55.0-61.0)** **82.63 ± 6.66** **(58.3-118.0)** **1.38 ± 0.64** **(1-3)**	n=496 58.79 ⊥ 1.08 (54.0-61.0) 83.56 ⊥ 6.89 (61.4-111.0) 1.38 + 0.64 (1-3)
≥ 120 (n_s=438)	n=214 59.00 + 1.09 (55.5-61.0) 84.00 + 6.86 (61.8-106.3) 1.30 ⊥ 0.59 (1-3)	n=889 59.11 + 0.96 (55.0-61.0) 82.95 + 6.40 (63.9-112.0) 1.37 ⊥ 0.61 (1-4)	n=959 58.81 + 1.05 (55.0-61.0) 82.95 + 6.80 (61.6-115.4) 1.37 ⊥ 0.61 (1-3)	**n=242** **58.26 ± 1.24** **(55.0-61.0)** **83.10 ± 6.52** **(68.1-107.7)** **1.33 ± 0.60** **(1-3)**

Suppl. Tab. 3. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for within litter variance of BMI of their parents ($RBV_{vBMI\ sire}$, $RBV_{vBMI\ dam}$), considering 14,416 male dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{vBMI\ sire}$	$RBV_{vBMI\ dam}$			
	< 80 (n_d=570)	80-99 (n_d=3,710)	100-119 (n_d=4,144)	≥ 120 (n_d=716)
< 80 (n_s=324)	**n=161**	n=828	n=907	n=267
	64.25 ± 0.91 (61.5-66.0)	64.41 ± 0.82 (60.0-66.0)	64.34 ± 0.87 (61.0-66.0)	64.16 ± 0.95 (61.0-66.0)
	87.95 ± 5.97 (71.0-104.2)	87.49 ± 6.13 (67.0-106.6)	88.12 ± 6.23 (66.3-107.1)	89.47 ± 6.70 (69.7-110.1)
	1.39 ± 0.62 (1-3)	1.40 ± 0.64 (1-3)	1.36 ± 0.59 (1-3)	1.32 ± 0.57 (1-3)
80-99 (n_s=1,397)	n=411	**n=2,464**	n=2,395	n=448
	64.30 ± 0.94 (60.0-66.0)	**64.42 ± 0.85 (59.5-66.0)**	64.41 ± 0.87 (60.0-66.0)	64.34 ± 0.91 (60.0-66.0)
	87.79 ± 6.00 (71.0-110.9)	**87.09 ± 5.99 (61.5-107.2)**	87.83 ± 6.33 (68.9-110.2)	88.33 ± 6.71 (66.3-105.3)
	1.40 ± 0.62 (1-3)	**1.38 ± 0.61 (1-4)**	1.41 ± 0.63 (1-3)	1.39 ± 0.61 (1-3)
100-119 (n_s=1,426)	n=341	n=1,841	**n=2,143**	n=365
	64.34 ± 0.91 (60.0-66.0)	64.38 ± 0.88 (60.0-66.0)	**64.37 ± 0.90 (60.0-66.0)**	64.32 ± 0.95 (60.0-66.0)
	87.93 ± 5.99 (71.9-105.0)	87.53 ± 6.34 (68.6-112.8)	**88.57 ± 6.46 (66.3-112.3)**	89.40 ± 6.96 (68.4-112.1)
	1.34 ± 0.61 (1-3)	1.37 ± 0.61 (1-3)	**1.37 ± 0.62 (1-3)**	1.32 ± 0.56 (1-3)
≥ 120 (n_s=362)	n=156	n=762	n=709	**n=218**
	64.21 ± 1.07 (60.0-66.0)	64.37 ± 0.86 (60.0-66.0)	64.31 ± 0.95 (59.0-66.0)	**64.17 ± 1.09 (60.0-66.0)**
	88.14 ± 6.30 (71.9-106.6)	88.20 ± 6.30 (71.9-106.6)	89.14 ± 6.51 (69.4-114.7)	**91.35 ± 8.06 (71.0-112.3)**
	1.40 ± 0.59 (1-3)	1.37 ± 0.62 (1-3)	1.37 ± 0.62 (1-3)	**1.38 ± 0.61 (1-3)**

Suppl. Tab. 4. Distribution of offspring phenotypes with respect to withers height (WH; first line), body mass index (BMI; second line) and score of canine hip dysplasia (CHD; third line) by the relative breeding values for within litter variance of BMI of their parents ($RBV_{vBMI\ sire}$, $RBV_{vBMI\ dam}$), considering 21,612 female dogs from birth years 1992 to 2003 with information on WH and BMI.

$RBV_{vBMI\ sire}$	$RBV_{vBMI\ dam}$			
	< 80 (n_d=722)	80-99 (n_d=4,941)	100-119 (n_d=5,305)	≥ 120 (n_d=869)
< 80 (n_s=373)	**n=226** **59.23 ± 0.97** **(56.0-61.0)** **83.79 ± 6.40** **(66.7-112.0)** **1.29 ± 0.56** **(1-4)**	n=1,258 59.30 + 0.89 (55.0-61.0) 82.52 + 6.01 (60.9-108.3) 1.38 ⊥ 0.61 (1-3)	n=1,395 59.17 + 0.94 (55.0-61.0) 83.22 + 6.55 (63.2-109.2) 1.34 ⊥ 0.58 (1-3)	n=324 59.14 + 1.06 (55.0-61.0) 84.16 + 6.93 (63.9-102.0) 1.32 ⊥ 0.58 (1-3)
80-99 (n_s=1,717)	n=591 59.22 ı 0.98 (55.0-61.0) 82.41 ⊥ 6.05 (65.0-101.6) 1.38 ⊥ 0.62 (1-3)	**n=3,819** **59.32 ± 0.86** **(55.0-61.0)** **82.25 ± 6.06** **(59.3-112.0)** **1.39 ± 0.64** **(1-3)**	n=3,458 59.26 ı 0.91 (55.0-61.0) 82.72 ⊥ 6.39 (62.5-115.3) 1.40 ⊥ 0.64 (1-4)	n=655 59.20 ı 0.95 (55.0-61.0) 82.83 ⊥ 6.68 (58.3-105.2) 1.37 ⊥ 0.62 (1-3)
100-119 (n_s=1,723)	n=472 59.15 ⊥ 1.01 (55.0-61.0) 83.20 ⊥ 6.35 (68.37-101.6) 1.32 + 0.60 (1-3)	n=2,876 59.24 ⊥ 0.92 (55.0-61.0) 82.37 ⊥ 6.19 (62.4-107.0) 1.37 + 0.62 (1-4)	**n=3,129** **59.17 ± 0.96** **(55.0-61.5)** **83.18 ± 6.77** **(60.1-115.4)** **1.36 ± 0.61** **(1-4)**	n=549 59.18 ⊥ 0.97 (55.0-61.0) 82.46 ⊥ 7.07 (64.6-116.4) 1.38 + 0.61 (1-3)
≥ 120 (n_s=423)	n=215 59.03 + 0.98 (55.0-61.0) 82.50 + 6.01 (65.0-104.0) 1.34 ⊥ 0.59 (1-3)	n=1,224 59.11 + 1.02 (55.0-61.0) 82.75 + 6.47 (58.3-108.3) 1.35 ⊥ 0.62 (1-4)	n=1,094 59.17 + 0.95 (55.0-61.5) 83.16 + 7.14 (61.1-120.0) 1.39 ⊥ 0.62 (1-3)	**n=327** **58.98 ± 1.09** **(54.0-61.0)** **84.02 ± 9.07** **(61.8-118.0)** **1.30 ± 0.56** **(1-3)**

CHAPTER 6

General discussion

General discussion

In dog breeding selection of mating partners based on different criteria, such as conformation, performance and health traits. Because dog breeding is always a multiple trait selection it was important to know whether there are relevant relationships between the considered traits, with a main focus on body measures and CHD, which could be used to improve future breeding success. The existence of a moderate to high heritability and clearness of trait definition for every breeding trait can be seen as a precondition for successful breeding, too. Therefore the objective of the present thesis was to analyze systematic and genetic effects on weight and body measures and their relationships with CHD in GSD. Also the expected selection response for conformation and conformational homogeneity of litters was analyzed and, with focus on CHD explicitly, the ability of PBV to predict offspring phenotypes was compared with selective breeding based on the CHD phenotype of the parents.

Dog breeding standards define the lower and upper limits of body measures that a dog requesting permission for breeding has to fulfill. In the present study mean WH for males and females and mean BW for females were close to the upper limits. But heritability estimates for both traits were high which was in agreement with findings of Helmink et al. (2001). These moderate to high heritabilities of body measures provide the basis for selective breeding towards for example smaller withers height or favorable body proportions and stature. The positive additive genetic correlations in the order from 0.91 to 0.98 between corresponding traits in males and females indicate an equal genetic basis of body measures in both sexes. It can therefore be concluded that selection for conformation traits will equally affect both sexes and will not increase sexual dimorphism in the dogs. Furthermore, future analyses of body measures could be performed for both sexes together.

To figure out relevant relationships between the body measures WH and BMI and the health trait CHD, body measures of 31,398 dogs and CHD scores of 105,756 GSD born between 1992 and 2003 were considered. Comhaire and Snaps (2008) analyzed the relationship of CHD and body measures between different dog breeds resulting in a significant and very high correlation between CHD and BMI. Our results implicate that across-breed relationships between CHD and BMI can not be directly transferred to within-breed relationships in the German population of GSD. We found positive, but very small phenotypic and genetic correlations between body measures and CHD in the German population of GSD. Therefore, WH and BMI may not be very useful as accessory traits for selection against CHD.

Nevertheless, CHD scores should be used to monitor possible side effects when multiple trait selection strategies with regard to different body measurements are evaluated. In the GSD current means of WH and BW are close to the upper limits defined in their standard. Concurrent selection for small WH and vWH was found to most efficiently reduce mean WH in males and females while having little impact on CHD distributions and is therefore recommended to maximize breeding success with regard to conformation and conformational homogeneity in the GSD.

Up to know we analyzed the relationships between body measurements and CHD, without evaluating the currently practiced selection scheme against CHD in the German population of GSD explicitly. Therefore the ability of PBV to predict offspring phenotypes was compared with selective breeding based on the CHD phenotype of parents. The proportion of explained phenotypic variance was lower than 1% for parent phenotypes and 2 to 3% for PBV. Therefore, genetic evaluation for CHD may help to select against CHD, but expectations regarding the selection response should not be too high. Several factors which relate to the genetic nature and the phenotypic characterization of CHD limit the predictability of phenotypes.

In the course of this study it was not possible to find conformation traits which may relevantly assist selection against CHD. However, genetic correlations between CHD and conformation traits were identified that should not be ignored in future dog breeding. Favorable conformation of dogs is defined in the breeding standards, so conformation must be considered in any breeding strategy. Genetic homogeneity between genders and high heritabilities facilitate conformation selection. Interference with selection against CHD as the most important health trait in the GSD should be avoided by concurrent consideration of all traits of selection relevance. Maximum breeding progress with respect to appearance, obedience and health will be achieved by multiple trait selection using genetic evaluation. PBV are currently used to assist selection against CHD, but prediction of BV may in the future also include conformation traits, such as height and weight, performance traits or other health traits, such as ED. Reliability of genetic evaluation will benefit from large scale availability of phenotype information on all traits which are considered relevant for selection. In the GSD, routine screening for skeletal health and conformation evaluation of large numbers of dogs provide a suitable basis for optimization of future breeding strategies.

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CHAPTER 7

Summary

Summary

Melanie Dammann (2009)

Analysis of systematic and genetic effects on weight and body measurements and their relationships with canine hip dysplasia in German shepherd dogs

The objective of the present thesis was to analyze systematic and genetic effects on weight and body measures and their relationships with canine hip dysplasia (CHD) in the German population of German shepherd dogs (GSD). Furthermore currently practiced selection strategies with respect to CHD were evaluated. Finally the diversity within litters with regard to body measures, which are part of the breeding standard, were analyzed. Because dog breeding is always a multitrait selection it was important to know whether there are relevant relationships between the analyzed conformation and health traits, such as CHD, which could be used to improve future breeding success.
Breeding standards for dogs usually define the lower and upper limits of body measures that a dog needs to fulfil to get the permission for breeding. Available data included conformation information from 36,028 breeding dogs born between 1992 and 2003 with measurements of withers height (WH), chest height, chest circumference and body weight (BW). Analysis of variance was performed for the systematic effects sex, birth year, month of birth, region, age at licensing, litter size and inbreeding coefficient. Birth year, month of birth, region and age of breeding approval were in most cases significant for the traits analyzed. Inbreeding coefficient was significant as a nonlinear covariate for withers height and chest circumference. The pedigree file used for the genetic analysis consisted of 574,356 registered animals born between 1985 and 2006. The genetic parameters were estimated in linear animal models using the residual maximum likelihood (REML). Uni- and bivariate analyses were performed for both sexes together and separately for males and females. The male dogs had a mean withers height of 64.4 cm and a mean body weight of 36.5 kg. Female dogs had a mean withers height of 59.2 cm and a mean

weight of 29.0 kg. Heritability estimates for both sexes together were 0.41 ± 0.01 for withers height and 0.27 ± 0.01 for body weight. For the other traits studied, heritability estimates were lower with values of 0.20 ± 0.01 for chest height and 0.13 ± 0.01 for chest circumference. In the separate analyses for male and female dogs, heritability estimates were higher for females. Additive genetic correlations in the order from 0.91 to 0.98 between corresponding traits in males and females indicated an equal genetic basis of body measures in both sexes. It can therefore be concluded that selection for conformation traits will equally affect both sexes and will not increase sexual dimorphism in dogs. Thus future analyses of body measures could be performed for both sexes together.

For the analyses of relationships between WH, Body Mass Index (BMI), i.e. the quotient of BW and squared WH, and CHD, body measures of 31,398 dogs and CHD scores of 105,756 GSD born between 1992 and 2003 were considered. The pedigree contained 141,100 animals, including ancestors for up to four generations and 6,175 base animals. Genetic parameters were estimated bivariately in linear animal models using Gibbs sampling with the program MTGSAM. Distribution of CHD scores in progeny by WH and BMI of their parents indicated that there was no obvious phenotypic correlation between CHD and body measures. Estimated additive genetic heritabilities of the animal were 0.18 ± 0.01 for CHD, 0.49 ± 0.04 for WH and 0.17± 0.02 for BMI. Given the low phenotypic and genetic correlations ranging between -0.07 and 0.07 between CHD on the one hand and WH and BMI on the other hand, it can be concluded that dog breeding with focus on CHD will have a very slight influence on body measures and vice versa. WH and BMI may not be very useful as accessory traits for selection against CHD.

In the GSD, selection against CHD is practiced for decades, but mass selection and pedigree breeding value (PBV) based selection for CHD have not yet led to satisfactory improvement of the CHD status in the German population of GSD (Janutta *et al*. 2008). To find reasons for the slow breeding progress the ability of PBV to predict offspring phenotypes compared with selective breeding based on the CHD phenotype of parents was investigated. Official scores for CHD of 184,489 GSD from birth years 1985 to 2007 were included in the genetic analyses. Pedigree

information on up to eight generations was considered, resulting in a relationship matrix of in total 200,853 dogs. Breeding values were predicted under the assumption of a heritability of CHD of 0.20 by Best Linear Unbiased Prediction (BLUP). Proportions of explained phenotypic variance lower than 1% for selection based on parent phenotypes only, and 2 to 3% for selection based on PBV explain the little success in CHD elimination. Therefore, selection using PBV maybe preferable over mass selection but selection response for CHD is limited.

In the GSD current means of WH and BW are close to the upper limits defined in their standard. Therefore, the expected selection response for conformation and conformational homogeneity was investigated. Body measurements were available for 36,028 dogs born between 1992 and 2003, 14,416 male and 21,612 female GSD from 26,155 litters. WH and BMI, i.e. the quotient of BW and squared WH, were considered as traits to directly select for certain size and stature. Within litter variance of WH (vWH) and BMI (vBMI) were defined as traits to select for conformation homogeneity of litters with at least two dogs with conformation data. To monitor possible side effects of conformation selection for CHD, CHD scores for all dogs were used. Genetic parameters were estimated multivariately in linear animal models using Gibbs sampling. Heritabilities ranged between 0.19 and 0.34 for all traits with additive genetic correlation of -0.11 between WH and vWH and 0.11 between BMI and vBMI. Breeding values (BV) for WH and BMI were negatively correlated with -0.20 in sires and -0.17 in dams. Expected selection response was studied using relative breeding values (RBV) of parents, assuming exclusion of sires and/or dams with RBV larger than 120, and comparing means of WH, BMI and CHD score between offspring of all and selected parents. Concurrent selection for small WH and vWH was found to most efficiently reduce mean WH in males and females while having little impact on CHD distributions. Multiple trait selection for WH, vWH, BMI and vBMI was hindered by the negative genetic correlations between the traits and tended to interfere with improvement of CHD status. Use of RBV for WH and vWH for conformation selection is therefore recommended to maximize breeding success with regard to conformation and conformational homogeneity in the GSD.

Routine screening for skeletal health, such as CHD and ED and conformation evaluation of large numbers of dogs provide a suitable basis for further optimization of future breeding strategies.

CHAPTER 8

Zusammenfassung

Zusammenfassung

Melanie Dammann (2009)

Populationsgenetische Analyse von Körpermaßen und deren Zusammenhang mit der Hüfgelenkdysplasie beim Deutschen Schäferhund

Ziel der vorliegenden Dissertation war es, die systematischen Einflussfaktoren für die bei der Körung erfassten Körpermerkmale beim Deutschen Schäferhund (DSH) und deren Zusammenhang mit der Hüftgelenkdysplasie (HD) zu klären und genetische Parameter zu schätzen. Außerdem wurde die Effizienz der aktuellen Zuchtstrategie gegen HD überprüft, sowie verschiedene Zuchtstrategien im Hinblick auf Exterieurmerkmale und geringe Wurfvarianz derselben beim Deutschen Schäferhund verglichen.

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Populationsgenetische Analyse von Körpermaßen beim Deutschen Schäferhund

Einleitung

In der Hundezucht erfordern Rassestandards bestimmte Grenzen bei den Körpermaßen einzuhalten, damit der Hund eine Zuchterlaubnis erhält. Ziel dieser Studie war es deshalb, die Bedeutung systematischer Einflussfaktoren für die bei der Körung erfassten Körpermerkmale beim DSH zu klären und genetische Parameter zu schätzen.

Material und Methoden

Zur Analyse der Körpermerkmale konnten Informationen zu Widerristhöhe, Brusttiefe, Brustumfang und Körpergewicht von 36.028 gekörten DSH über einen Zeitraum von 10 Jahren (Geburtsjahrgänge 1992-2003) untersucht werden. Für die genetischen Analysen standen die Abstammungsdaten für 547.356 Hunde der Geburtsjahrgänge 1985-2006 zur Verfügung. Die Schätzung genetischer Parameter

im linearen Tiermodell erfolgte mittels Residual Maximum Likelihood (REML). Die uni- und bivariaten Analysen wurden zum einen geschlechtsübergreifend und zum anderen, getrennt nach Geschlecht durchgeführt.

Ergebnisse und Diskussion

Die Heritabilität in der geschlechterübergreifenden Auswertung betrug für das Körpergewicht 0,27 ± 0,01 und für die Widerristhöhe 0,41 ± 0,01. Für die Brusttiefe und den Brustumfang lagen die Heritabilitätsschätzwerte mit Werten von 0,20 ± 0,01 und 0,13 ± 0,01 niedriger. Hündinnen zeigten bei der Analyse getrennt nach Geschlecht für alle Merkmale höhere Heritabilitäten als Rüden. Die genetischen Korrelationen zwischen entsprechenden Merkmalen bei Rüden und Hündinnen waren mit Werten von 0,91 bis 0,98 für alle Merkmale sehr hoch. Damit ist zu erwarten, dass eine Selektion auf Körpermerkmale beide Geschlechter gleichmäßig beeinflusst und den Geschlechtsdimorphismus nicht verstärkt. Zukünftige Analysen von Körpermerkmalen können demzufolge geschlechtsübergreifend durchgeführt werden.

Analyse von genetischen, phänotypischen und umweltbedingten Einflüssen auf das Körpergewicht und Körpermerkmale und deren Zusammenhang mit der Hüftgelenkdysplasie beim Deutschen Schäferhund

Einleitung

Ein Zusammenhang zwischen Körpermaßen, wie Widerristhöhe (WH) und Body Mass Index (BMI), und HD wurde in verschiedenen Studien diskutiert. Ziel der vorliegenden Studie war es zu untersuchen, ob beim DSH ein Zusammenhang zwischen Körpermerkmalen und HD besteht, der zur Selektion gegen HD genutzt werden könnte.

Material und Methoden

Die ausgewerteten Daten umfassten 105.756 HD-untersuchte zwischen 1992 und 2003 geborene und beim Verein für Deutsche Schäferhunde (SV) e.V. registrierte Deutsche Schäferhunde. Für 31.398 Hunde lagen Informationen zu den

Körpermaßen WH und BMI vor. Für die Schätzung genetischer Parameter wurden Abstammungsinformationen über vier Generationen einbezogen. Damit gingen Verwandtschaftsinformationen zu 141.000 Hunden, darunter 6.175 Basistiere in die Analysen ein. Die Schätzung genetischer Parameter erfolgte unter Berücksichtigung maternal-genetischer Effekte im linearen Tiermodell unter Verwendung von Gibbs Sampling mit dem Programm MTGSAM.

Ergebnisse und Diskussion

Die geschätzte additiv genetische Heritabilität des Tieres betrug 0.18 ± 0.01 für HD, 0.49 ± 0.04 für WH and 0.17± 0.02 für BMI. Auf Grundlage der niedrigen phänotypischen und genetischen Korrelationen von -0.07 bis 0.07 zwischen HD und BMI und zwischen HD und WH ist zu erwarten, dass die Einbeziehung von WH und BMI als Hilfsmerkmale zur Selektion gegen HD den Zuchtfortschritt in der deutschen Population des DSH nicht steigern würde.

Untersuchungen zur Aussagekraft der Vorhersage von Pedigreezuchtwerten für Hüftgelenkdysplasie beim Deutschen Schäferhund

Einleitung

In der deutschen Population Deutscher Schäferhunde gelten seit den 1960er Jahren Zuchtbestimmungen gegen HD. Die seit 1966 angewendete phänotypische Massenselektion wurde 1999 durch die Einführung von Best Linear Unbiased Prediction (BLUP) Methoden zur Zuchtwertschätzung ergänzt. Hierbei wurden Pedigree-Zuchtwerte (PZW) im linearen Tiermodell unter Berücksichtigung aller Verwandtschaftsbeziehungen geschätzt. Aus früheren Studien ging hervor, dass der Zuchtfortschritt bezogen auf HD, sowohl für die phänotypische Massenselektion als auch für die Zuchtwertschätzung in verschiedenen Hunderassen, auch dem DSH, bislang nicht zufrieden stellend ist (Flückiger *et al*. 1995; Swenson *et a*l. 1997; Leppänen and Saloniemi 1999; Hamann *et al*. 2003; Janutta *et al*. 2008). Deshalb war das Ziel der Studie, zu vergleichen wie zuverlässig Nachkommenphänotypen mit Hilfe von PZW oder auf Basis der Phänotypinformationen der Eltern vorhergesagt werden können.

Material und Methoden

Für die genetischen Analysen wurden HD-Befunde von 184.489 DSH, die zwischen 1985 und 2007 geboren wurden, berücksichtigt. Die Verwandtschaftsmatrix umfasste 200.853 Hunde aus 8 Generationen mit 12.307 Basistieren. Die Zuchtwerte auf Grundlage einer Heritabilität von 0,20 mittels BLUP unter der Verwendung des Programms PEST, Version 4.2 (Groeneveld 1990). Für die Schätzung der Pedigree-Zuchtwerte wurden die HD-Befunde der Eltern und aller weiteren Verwandten einbezogen, außer des HD-Befundes des Probanden selbst und aller Verwandten aus demselben Geburtsjahr. D.h. für alle Hunde eines jeden Geburtsjahres wurden PZW, unter Verwendung aller verfügbaren HD-Befunde und Pedigreeinformationen bis zum Jahr der Geburt des Probanden, geschätzt.

Ergebnisse und Diskussion

Der Anteil erklärter phänotypischer Varianz war niedriger als 1%, wenn die Selektion nur auf dem Phänotyp der Eltern, d.h. auf Massenselektion, basierte. Ein sehr niedriger Anteil von 2% bis 3% durch Pedigree-Zuchtwerte erklärter phänotypischer Varianz entspricht dem bislang geringen Selektionserfolg gegen HD. Folglich ist die Selektion gegen HD mit Hilfe von Pedigree-Zuchtwerten der phänotypbasierten Massenselektion vorzuziehen, aber dennoch limitiert.

Untersuchungen zur Möglichkeit der Selektion auf Exterieurmerkmale und geringe Wurfvarianz beim Deutschen Schäferhund

Einleitung

In der Schäferhundzucht haben sich die Körpermaße Widerristhöhe und Körpergewicht bei den gekörten Rüden und Hündinnen den vom Rassestandard vorgegebenen oberen Grenzen angenähert. Um den Anteil der Hunde, die dem Rassestandard entsprechen, künftig zu steigern, wurden verschiedene Zuchtstrategien im Hinblick auf Exterieurmerkmale und geringe Wurfvarianz derselben beim Deutschen Schäferhund verglichen.

Material und Methoden

Für 31.398 Deutsche Schäferhunde (DSH) aus den Geburtsjahrgängen 1992 bis 2003 lagen Informationen zu den Körpermaßen Widerristhöhe (WH) und Body Mass Index (BMI) vor. Die Definition der Merkmale Wurfvarianz für WH (vWH) und Wurfvarianz für BMI (vBMI) erforderte das Vorliegen von Körpermaßen für mindestens zwei Wurfgeschwister, so dass hierfür Informationen von 17,154 DSH genutzt werden konnten. Die Schätzung genetischer Parameter erfolgte multivariat im linearen Tiermodell mittels Gibbs Sampling, wobei jeweils ein Körpermaß und seine Varianz innerhalb eines Wurfes einbezogen wurden. Unter Berücksichtigung von Abstammungsinformationen über vier Generationen umfasste die Verwandtschaftsmatrix insgesamt 65.551 Hunde, darunter 12.249 Basistiere. Die Untersuchung des erwarteten Erfolges einer Selektion auf Exterieur bzw. geringe Varianz des Exterieurs innerhalb der Würfe erfolgte anhand der für die Eltern der Hunde mit Exterieurinformationen geschätzten Zuchtwerte. Um eine Verminderung von WH und BMI bzw. eine größere Einheitlichkeit der Würfe in Bezug auf WH und BMI zu erzielen, wurde ein Ausschluss von Eltern mit einem Zuchtwert von über 120 für das entsprechende Merkmal angenommen. Verglichen wurden dann die Verteilungen von WH und BMI unter den Nachkommen der derart selektierten Eltern mit den entsprechenden Verteilungen bei allen Hunden mit bekannten Körpermaßen. Mögliche Nebeneffekte einer solchen Exterieur-Selektion auf das Auftreten der Hüftgelenkdysplasie (HD), gegen die beim DSH bereits selektiert wird, wurden durch entsprechenden Vergleich der HD-Grad-Verteilungen untersucht.

Ergebnisse und Diskussion

Die Heritabilitätsschätzwerte lagen für alle untersuchten Merkmale zwischen 0,19 und 0,34 die additiv genetischen Korrelationen betrugen -0,11 zwischen WH und vWH und 0,11 zwischen BMI und vBMI. Die für die Eltern der Informanten geschätzten Zuchtwerte für WH und BMI waren mit -0,20 bei den Väter und -0,17 bei den Müttern negativ korreliert. Bei einer Selektion auf nur eines der beiden untersuchten Körpermaße ist sich demnach kein Zuchtfortschritt in Bezug auf WH und BMI zu erwarten. Die gleichzeitige Reduktion von WH und vWH erfordert ebenso die Berücksichtigung beider Merkmale bei der Auswahl von Elterntieren. Am effizientesten ließ sich die mittlere WH bei Rüden und Hündinnen durch eine gleichzeitige Selektion auf kleine WH und kleine vWH reduzieren. Relevante Auswirkungen auf die HD-Verteilung sind dabei nicht zu erwarten. Im Gegensatz dazu wurde die gleichzeitige Berücksichtigung aller vier in die Untersuchung einbezogenen Merkmale (WH, vWH, BMI, vBMI) durch die negativen genetischen Korrelationen erschwert, und es deutete sich ein eher ungünstiger Effekt auf die HD-Verteilung an. Um einen maximalen Zuchtfortschritt in Bezug auf die im Rassestandard des DSH aufgeführten Exterieurmerkmale zu erzielen und die Einheitlichkeit des Exterieurs innerhalb der Würfe zu erhöhen, empfiehlt sich daher die Einbeziehung von Zuchtwerten für WH und vWH bei der Zuchttierauswahl.

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