The correlation between inbreeding and performance in the Hanoverian Sport Horse.

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Abstract

The aim of this thesis was to examine the relationship between inbreeding and performance in the Hanoverian Sport Horse.

A total of 84,724 hanoverian horses born between the years 1990 and 2009 were used for the study, of which 78,907 had their own performance records. Pedigree records were traced back as far as possible, with a maximum of 37 generations used. There was 100% completeness of pedigree up to the grandparent generation for all horses. The majority of horses (80%) had completeness of pedigree past the sixth generation.

Inbreeding were calculated using two methods; the Meuwissen method and the van Raden Method. Both methods gave identical results (100% fit). As aquantitative measure of performance, the Integrated Estimated Breeding Value (iEBV), using both breed and competition results was used. The Evaluation was carried out using the BLUP (Best Linear Unbiased Prediction) Multitrait Repeatability Animal Model. Two different GLM were run with the inbreeding coefficient (IBC) modelled as either a continuous variable or as a fixed class of five differing levels of inbreeding (IBC=0.00; 0<IBC≤0.01: 0.01<IBC≤0.02; 0.02<IBC≤0.05; 0.05<IBC). Age and Sex were included as fixed effects within the model.

All subgroups in both dressage and jumping data, with either fixed effect or linear covariate for the IBC, generated a similar result. Due to the large sample size there was a significant (p<0.001) relationship between inbreeding (IBC) and performance (iEBV). In dressage horses there was a significant positive relationship in all categories while in jumping horses there was a significant negative relationship in all catagories. However, the effect of inbreeding on iEBV explained only ±1% of the variance in the models. The models were simultaneously adjusted for the bias of the confounding factor of sex which also accounted for ±1% of the variance. The majority of variance in iEBV is due to the year cohort effect which accounts for ± 95%. The low level of inbreeding (±1.5%) and lack of biological effect on iEBV indicate that inbreeding is not a problem in the Hannoverian horse.

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List of abbreviations and terms

APB	(Aufbauprüfung) Sport events – show jumping and dressage of Young Horses' competitions,
ATSE	Accumulated, transformed and standardized earnings
BLUP	Best Linear Unbiased Predictor Multi-trait–Repeatability–Animal Model
$BYEAR_k$	fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008- 2009)
CPT	Central performance tests
DF	Degrees of freedom
DKB-Bundeschampionate	The German Championships of Young German Horses and Ponies
Dressage horses	Refers to the dressage data of the relevant horse subgroup
DWB	Dutch Warmblood horse
eijkl	Random residual
F	Coefficient of inbreeding as defined by Sewall Wright
F_A	Inbreeding Coefficient of the common ancestor
F_x	Inbreeding Coefficient of individual horse
FE	Fixed effect
FEI	Federation Equestre Internationale
FN	Fédération Equestre Nationale (Germany)
GLM	General Linear Model
H^2	Heritability
HLP	(Hengstleistungsprüfung) Stallion performance test.
i	Intensity of selection of genetic gain

IBC	Inbreeding coefficient
IBCi	Inbreeding coefficient of $horse_i$
$IBCC_i$	Fixed effect of inbreeding coefficient class (i=1-5; IBC=0.00, 0.00 < IBC ≤ 0.01, 0.01 < IBC ≤ 0.02, 0.02 < IBC ≤ 0.05, IBC > 0.05)
iEBV	Integrated Estimated Breeding Value
IGE	Integrated Genetic Evaluation
IHB	Irish Horse Board
Jumping Horses	Refers to the jumping data of the relevant horse subgroup
KWPN	Royal Dutch Sport Horse
LC	linear covariate
Meuw.f	The Meuwissen method for computation of inbreeding coefficients
MPT	iEBV for mare performance test
MPTD	iEBV for dressage in mare performance test
MPTJ	iEBV for jumping in mare performance test
N	Number of horses in relevant subgroup
n_1	Number of generations from the sire to the common ancestor
n_2	Number of generations from the dam to the common ancestor
p	P-value
Pr	"The probability of"
PEDIG	Fortran 77 software package used for computation of inbreeding coefficients
r	Accuracy of selection of genetic gain
R^2	R-squared
RF	Rasmussen Factor
rg	Genetic Correlation
SEXj	Fixed effect of sex

S.D.	Standard Deviation
SF	Selle Français horse
SPT	iEBV for stallion performance test.
SPTD	iEBV for dressage in stallion performance test.
SPTJ	iEBV for jumping in stallion performance test.
SS	Sum of Squares
SWB	Swedish Warmblood horse
T	Generation interval
TC	iEBV for Tournament competitions
TCD	iEBV for tournament competitions dressage
TCJ	iEBV for Tournament competitions jumping
TI	Total Index
TID	Total Index Dressage
TIJ	Total Index Jumping
TIMEFORM	Relates to Timeform Publications and is a publishing company in Halifax, West Yorkshire, England as used by the racing industry to produce information and statistics on individual racehorses.
TORIS	Turnier ORganisations und Informations System
TSP	(Turniersportprüfung) Sport events - show jumping and dressage competitions.
V_P	Phenotypic variation
V_G	Variation in genetic values
VA	(Veranlagungsprüfung) ability test of young stallions,
vanrad.f	The van Raden method for the computation of inbreeding coefficients
YC	iEBV for Young Horse competitions

YCD	iEBV for Young Horse competitions dressage
YCJ	iEBV for Young Horse competitions jumping
yijkl	Breeding value (iEBV)
ZSP	(Zuchtstutenprüfung) Own performance test of mares,
μ	Model constant

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Heritability

$H^2 = V_G/V_P$

H = Heritability

V_P = phenotypic variation

V_G = Genotypic variation

coefficient of inbreeding (F) defined by Sewall Wright in the early 1920s

$$F_X = \sum\left[\left(\frac{1}{2}\right)^{n_1+n_2+1}(1+F_A)\right]$$

F_x = Inbreeding Coefficient of individual horse

F_A = Inbreeding Coefficient of the common ancestor

n_1 = Number of generations from the sire to the common ancestor

n_2 = Number of generations from the dam to the common ancestor

List of Models

$y_{ijkl} = \mu + b\ IBC_i + SEX_j + BYEAR_k + e_{ijkl}$

y_{ijkl} = breeding value (iEBV)

μ = model constant

IBC_i = inbreeding coefficient of $horse_i$

SEX_j = fixed effect of sex

$BYEAR_k$ = fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008-2009)

e_{ijkl} = random residual

$y_{ijkl} = \mu + IBCC_i + SEX_j + BYEAR_k + e_{ijkl}$

y_{ijkl} = breeding value (iEBV)

μ = model constant

$IBCC_i$ = fixed effect of inbreeding coefficient class (i=1-5; IBC=0.00, $0.00 < IBC \leq 0.01$, $0.01 < IBC \leq 0.02$, $0.02 < IBC \leq 0.05$, $IBC > 0.05$)

SEX_j = fixed effect of sex (j=1-2; stallions, mares)

$BYEAR_k$ = fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008-2009)

e_{ijkl} = random residual

Chapter 1: INTRODUCTION

Horse breeding in Europe has evolved over time from the form of the draught horses to the iconic Sport Horses seen in competitions today, as such, entailing a change in phenotypes and subsequent genotypes (Langlois, at al. 1983). The transformation was assisted by modern animal breeding theory, which involved the use of objective instruments for measuring important traits and the development of indices as criteria for a more effective selection of breeding animals (Àrnason, et al. 1994). This process has involved utilizing superior stallions, at times more than once in a pedigree, to improve phenotypic aspects considered important to the performance of the breed type (Azevedo and Barata, 1982). Early authors proposed the use of inbreeding (Tesio, 1947), however modern findings have indicated the inaccuracy of said inbreeding theory, as has been observed in production traits (Ercanbrack and Knight, 1991; Miglior and Burnside, 1995) (Thompson and Everett, 2000). Previous considerations have illustrated that researchers prior to the 1950's supported the ideology of inbreeding (Fletcher, 1946; Pearson, 2011; Rhoad & Kleberg, 1946 and Wright, 1921), whereas, researchers after 1950 coined the term 'inbreeding depression' after observations of the negative impacts and consequences of inbreeding, (Cothran, 1984; Klemetsdal, 1998; Rozhdestvenskaya, 1972; Sevinga, et al., 2004; Strom, 1982; van Eldik, et al., 2006 and van Raden, 1992). Inbreeding depression refers to an increase in undesirable recessive disorders, a loss in genetic variation and a decrease in performance of the animals. Despite this, it is a commonly held belief among modern breeders that inbreeding to superior animals will produce a higher chance of breeding superior individuals (Roman, 2015). An early advocate of inbreeding in the Thoroughbred was the Italian Federico Tesio (1869-1954), whom developed a successful inbreeding principle, breeding the winners of 24 Italian Derby races between 1911 and 1966 (Tesio, 1947). This inbreeding principle, involving guidelines for linebreeding horses, is a representative yardstick for breeding, hence, still present in modern breeding programmes (Klemetsdal G, 1989 and Rozhdestvenskaya, 1972), especially with regards to the Warmblood horse (Niemann B, 2009).

Chapter 2: LITERATURE REVIEW

2.1 Measurement of performance in horses

Due to the intrinsic nature of performance in horse racing and the use of handicapped races, the Thoroughbred industry has developed an accurate measure of performance (Langlois, et al. 1983). In this regard, performance is a combination of measurements that involve the speed of the race, the weight the horse is carrying and the number of lengths ahead or behind the average horse in the race. The level of the race is assessed at the end of a season by the mean value of participating horses. This is expressed by a handicap value utilized in certain races (Gillespie, 1971; Langlois, et al. 1983). It is suggested that 5-6 races are needed to establish a horses' correct handicapping (Langlois, et al. 1983).

In Sport Horses, performance testing procedures vary depending on the breeding scheme and breeding population (Ström, 1978). Despite differences in testing protocol, Thorén Hellsten et al., (2006) reported that for the major European horse populations the results, as they relate to the assessment of individual stallion performance tests, were in good agreement. Sport Horse breed organisations use three types of tests to record performance data: station performance tests, field performance tests and competition tests (Bruns and Fredricson, 2001).

Horses are usually selected early in life on their own performance and to a large extent their pedigree for the discipline to which they are trained (Philipsson, 1990). Philipsson (1990) suggested that 73% of Swedish Warmbloods were trained for Show Jumping, 43% were trained for dressage, 7% for eventing, 1% for driving and 24% trained for more than one discipline. This predetermined selection may cause severe bias in studies of genetic parameters based on the performance data (Philipsson et al., 1990). An inherent inaccuracy of such lists is the fact that not always the best horses will make it to top-level competition. A number of factors may influence the results of genetic worth based on competition data. These include;

- Many horses are eliminated early in their career due to injury.
- Talented horses may not have the best riders available to take them to the top.
- Access to the correct trainer is imperative.
- Good horses may be exported, and thus their performance data is not made available for comparative analysis.
- Some stallions, after they prove their worth in a station performance test, are then "retired" as breeding stallions, and thus no competition data would be gained.

2.2 Indirect, Direct and combined selection

Indirect selection utilises mechanisms such as the central performance test and the prediction of performance based on certain conformation, movement and temperament "scores" assigned to a predetermined selection criteria (Gerber Olsson, et al., 2000; Koenen and van Veldhuizen, 1995), whereas Direct selection is simply the use of competition data to establish performance levels (Wallin, et al., 2003).

2.2.1 Indirect

In Germany and the Netherlands, stallions are selected via central performance tests (CPT) at special test stations that are run for usually 70 days but can run up to 120 days (Bruns and Fredricson, 2001; Huizinga, 1990) for the direct comparison of different stallions (Dubois, et al., 2008). In doing so, the process permits the measurement of a large number of traits (Brockmann, 1997; Koenen and Alridge, 2004). A further advantage of CPT are that horses are trained and judged under uniform conditions to minimize the effects of rider and pre-training (Bruns and Schade, 1998; Huizinga, et al., 1991). This is reflected with the higher heritabilities from performance testing at stations for both mares and stallions, than that of competition-based estimates of the same trait (Brockmann and Bruns, 2000; Von Velsen-Zerweck and Bruns, 1997).

In most German Warmblood associations, Centralised Performance Tests (CPT) involve estimates of traits assessed that are measured or graded using a numerical "score" between one and ten (Dorofejew and Dorofejewa, 1976; Ducro, et al., 2007; Gerber Olsson, et al., 2000; Langlois B, 1978; Müller and Schwark, 1979).

An alternative approach is the linear assessment system utilised by the Dutch Warmblood association (KWPN). Within the linear score system the horses are marked on their positive (or negative) deviation from the population mean in an attempt to provide data with a normal distribution (Koenen and van Veldhuizen, 1995).

Conformation, movement and jumping are the three main attributes tested in station and field performance tests (Dolvik and Klenetsdal, 1994; Langois, 1979). Conformation and movement tests conducted in test stations have positive correlations with performance in the dressage discipline (r_g~0.68) (Ducro, 2007). In contrast the correlation of conformation and movement with performance in show-jumping were low (r_g~0.26). This correlation in jumping was mainly due to the canter aspect of the appraisal as the walk and trot were very low (r_g~-0.14 to -0.04)

It is generally accepted that correct conformation is the basis for correct movement, which leads to positive performance as form follows function. However it seems that conformation may have less influence than is generally anticipated. Koenen and van Veldhuizen, (1995) and Burczyk (1989) deduced that the information of linear scored conformation scores is of minor importance with regards to indirect selection for performance. Showjumping especially seems to have significantly low correlation with conformation. Uphaus (1994) showed negative, close to zero or zero correlations between most gait traits and show jumping performance. Dušek, et al., (1970) also concluded that movement constitutes an inadequate measurement of performance in jumpers. Langlois (1978), however, found a favourable correlation between a long, strong croup and showjumping performance. In dressage horses, Holmström et al., (1990) indicated a positive genetic correlation of a long sloping shoulder.

While it seems that the relationship between conformation, movement and performance is at best arguable, Dubois and Ricard (2007) proposed that selection based on breeding values that include only performance values measured during a station test may result in a decrease in the potential genetic response by 53.1%.

2.2.2 Direct

Competition performance results are widely used in the genetic evaluation of showjumpers and are generally quantified using log of earning or log of earnings per start (Aldridge et al., 2000; Brockmann and Bruns, 2000; Reilly et al. 1998; Tavernier, 1990). However, Dubois and Ricard (2007) argued that competition tests might have inherent inaccuracies due to the fact that only a small number of horses are in competition.

Tavernier (1990) proposed that the only repeatable variable with competition results are the actual ranking of the horses compared to others in the competition as it is difficult to quantify level of jumps, faults and course difficulty. Based on data from 18,798 French jumping horses, it was estimated that performance based on rankings had a repeatability of 0.29.

Several authors advocate direct selection for sport performance in dressage and jumping with the standardised use of earnings for establishing performance (Bruns et al., 1978;Gomez, et al. 2011; Hintz, 1980; Klemetsdal, 1990; Langlois, 1980; Langlois, et al. 1983; Ricard and Chanu, 2001).

2.2.3 Combination

The Sport Horse breeder is often selecting for multiple phenotypic traits, in order to produce an individual with superior performance.

A combination of data sources, such as competition and performance tests, increase the accuracy of the resulting selection (Olsson, 2006). Philipsson et al., (1990) therefore proposed that the following points should be taken into account during selection:

- The effect of selection for conformation only at an early age vs. a step-wise selection, including performance test at a later stage on traits characterising conformation and competitive ability in dressage and jumping.
- The relative importance of performance tests of stallions vs. selection based on competition results at advanced levels at an older age.
- The relative importance of performance tests of mares.
- The correlated responses in different traits as a result of various definitions of the breeding objectives i.e. single-purpose vs. all-purpose horses.
- The importance of an early performance test for stallions.

Further, Olsson (2006) found that in the Stallion Performance Test analysis, the inclusion of performance of relatives' competition data for both dressage and jumping increased the mean accuracy for both the respective traits. Inclusion of competition results for the showjumping trait increased accuracy by 13% for stallions born in Sweden and 5% for stallions born outside Sweden. With the inclusion of dressage related competition Data, the "dressage trait" accuracy increased by 39 % for the stallions born in Sweden and 11% for the stallion born outside of Sweden.

Dubois (2008) presented a model for assessing performance of jumping Sport Horses that makes use of selection objectives, which included three trait groups;

- Conformation and gaits (weighted 20%).
- Competition jumping (weighted 60%).
- A third trait group (weighted 20%), such as; sperm quality or orthopaedic status.

The model then utilizes a four stage selection process including;

- A pedigree analyses.
- A performance test.

- Selection of males allowed to breed.
- Performance of offspring.

The annual genetic response for the model was 9.4% genetic standard deviation, with 2.6% for “conformation and gaits”, 9.0% for “Competition jumping”, and 1.5% for the “third trait”.

The disadvantage of considering a multiple trait breeding objective is that the genetic improvement per trait in absolute biological units can be considerably lower when compared to single trait breeding goals (Koenen and Alridge, 2004). In Foote’s (2002) study of Bovine breeding, it is shown that when selection is made for more than one trait, the genetic gain for each other trait is reduced, further illustrating that breeding for individual traits cannot be done in isolation. By implication, diminished genetic gain by multiple trait selection implies a decreased generation interval relating to overall genetic gain.

2.3 Young Horse competitions and progeny testing

In equestrian sports, “Young Horses” are referred to as 4, 5 and 6 year old individuals (FEI, 2015). Young Horse competitions are restricted to horses of the same year cohort and are designed to provide a modified competition format that reflects the age and stage of the training of the Young Horse.

Studies have shown a high genetic correlation ($r_g = 0.84$) in Warmbloods between observations at station performance testing of stallions and competition results of their offspring (Bruns, 2004).

Utilizing the measure of earnings/placings, with results at competitions later in life (0.68-0.88) Thorén Hellsten et al., (2006), measured traits recorded at Young Horse competitions as having good heritability (0.11 – 0.33) and high genetic correlations (0.68-0.88). In French Young Horse competitions, Tavernier (1992) estimated the heritability’s to be 0.33 for 4 year olds and 0.22 for 6 year old jumping horses while in Germany, Luehrs-Behnke and Roehe (2002) estimated heritability’s for horses in Young Horse competitions to be 0.12 for dressage and 0.11 for showjumping.

Station performance testing of progeny allows for the estimation of breeding values on stallions three to four years earlier than from progeny competition results (Christmann et al., 1995; Olsson and Arnason, 2000).

2.4 Integrated Estimated Breed Value (iEBV)

In Germany, the integrated Estimated Breeding Value (iEBV) model is based on a multiple-trait animal model, utilising performance testing of stallions in station, performance test of mares and the competition results of Sport Horses (Luehrs-Behnke and Roehe, 2002; Schöpke at al., 2013)

The traits used in the iEBV model include:

- Walk, trot, canter, rideability and free jumping data from mare performance test.
- Walk, trot, canter, rideability, free jumping and jumping under rider data from stallion performance test.
- Dressage and show jumping competition data for Young Horses.
- Dressage competition data.
- Show jumping competition data.

2.4.1 BLUP (Best Linear Unbiased Prediction)

The evaluation of the iEBV model calculated annually on behalf of the Fédération Equestre Nationale (FN) is carried out using the BLUP–Multi-Trait–Repeatability–Animal Model.

The BLUP (Best Linear Unbiased Predictor) was derived by Charles Roy Henderson in 1950 (van Vleck, 1998) and has since been used for genetic evaluations in most countries (Gomez et al., 2011)

Hugason et al., (1987) concluded that selection on the basis of estimated breeding values (iEBV) using the BLUP method across stallion age classes would result in genetic gain close to the maximum, and thus, breeders should be encouraged to make use of the estimated breeding values (iEBV) in their breeding plans.

2.5 Artificial insemination

The advent of artificial insemination and its use in Warmblood breeding has resulted in the utilisation of outside stallions in the Hanoverian population (referred to as non-Hanoverian stallions), increasing from 20% in 1990 to 40% in 2009 (Schade, 2010). Most Warmblood breed societies, including the Hannoveraner Verband, have moved toward the extensive use of artificial insemination (Niemann, 2009), and in doing so, there has evolved a need for breed societies to defend their identity as distinct “breed types”, due to an increase in utilisation of sires across breed societies.

The widespread use of artificial insemination and advancement in marketing techniques have resulted in the majority of stallions producing fewer progeny as breeders are no longer restricted to using stallions residing in their particular breeding area and are able to breed with elite stallions from across the globe. Approximately 50% of the available Hanoverian approved stallions had 4 or less registered progeny in 2006, where as in 1986 the median was 12 progeny per stallion (Niemann, 2009), indicating that with a similar number of foals produced, a smaller pool of stallions are breeding more foals.

2.6 The structure of studbooks - Breed vs Breed Type.

A primary focus of Sport Horse Societies is to increase the performance of Sport Horses, in a limited time frame, through increased genetic gain (Koenen and Alridge, 2004). This raises the discussion of a distinctive difference when considering breed over breed type: namely the speed at which the aims of the society’s breeding goals are realised. A “breed” society is restricted in that they have to protect the specific genetics of the breed (such as the Trakehner breed), whereas the “breed type” society has the freedom to utilise relevant “outside sires” to realise an immediate improvement of genotype. The Hanoverian is a “breed type”, allowing its members to breed with approved “outside” stallions.

Given the large exchange of genetic material between the Warmblood studbooks there is a trend for less distinct differences in phenotype or genotype breed regions or studbooks. This is not surprising given the similarity in the breeding objectives and in Germany the adoption of a universal riding horse breeding objective by most of the regional breed societies (Haring, 1980).

The large inter exchange of genetic material was documented by Koenen et al., (2004). They reported that the percentages of mares covered by an outside stallion for KWPN (Royal Dutch Sport Horse), DWB (Dutch Warmblood horse), SWB (Swedish Warmblood horse), SF (Selle Français horse) and IHB (Irish Horse Board) were: 31%, 74%, 62%, 6% and 32%, respectively. This indicates a strong tendency toward genetic exchange between the societies and dilutes any argument of distinctive “Breed types”.

2.7 Genetic gain – The generation interval and it's influence.

The French Selle Francais (SF) breeding program, which focuses specifically on the jumping horses, has shown a consistent increase in annual genetic gain (Dubois and Ricard, 2007). Dubois and Ricard (2007) explored the efficiency of the French Sport Horse jumping program and calculated the genetic gain of showjumping, eventing and dressage between 1974 and 2002 for the Selle-Francais (SF) (*figure* 1).

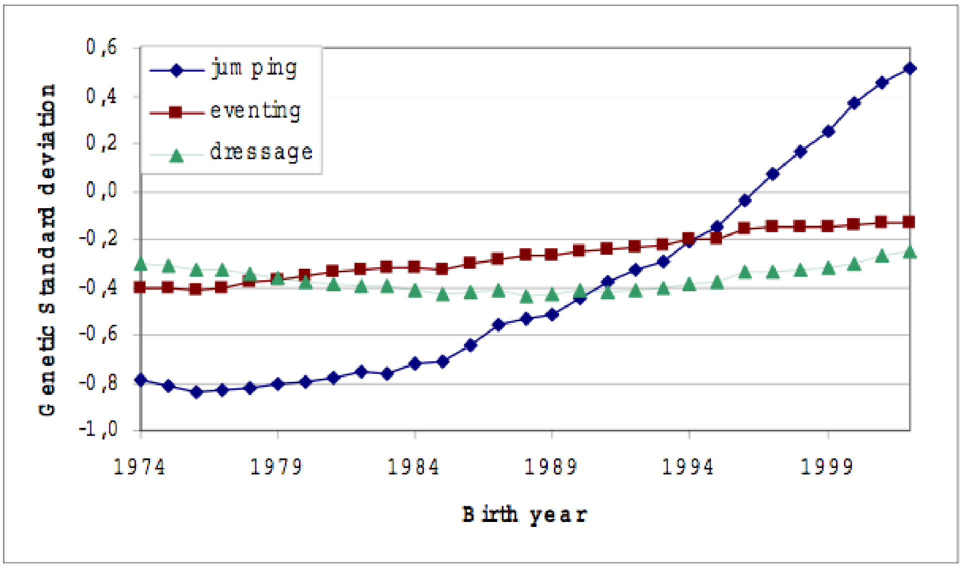

Figure 1: Estimated relationship between the birth year and the genetic standard deviation of jumping, eventing and dressage horses in the the Selle Francais (SF) horse population (1974- 2002) (Dubois and Ricard, 2007).

Using the The French Selle Francais breeding program, Dubois and Ricard (2007) ascertained the following parameters to describe the selection and industry structure;

1. The intensity of selection of genetic gain (i = 1,95 for males and 0.56 for females).
2. The accuracy of selection of genetic gain (r = 0.71 for males and 0,57 for females).
3. The generation interval (T = 12.9 years for a sire to breed sire; 10,4 years for a dam to breed a sire; 12,1 years for a sire to breed a dam; 11.4 years dam/dam).

In most breed societies, station performance tests are performed with horses aged between 3 and 6 years of age. This evaluation uses data obtained in a relatively short interval of time at a young age compared to competition data, which in turn generates shorter generation intervals, thus creating greater genetic gain (Stewart et al., 2010). Comparatively, Ducro et al., (2007) suggested that in a direct selection breeding scheme, using only the highest results in regular competition, it is not efficient as the results in high-level competitions can only be recorded at older ages (greater than 8 years), which further increase the generation interval.

Niemann (2009) suggested that within the Hanoverian Sport Horse population, the generation interval has decreased on the stallion side (from 12,4 (1970-1974) to 9,9 years (2000-2004)) and increased on the mare's side (from 8,6 (1970-1974) to 9,7 years(2000-2004). This could be indicative of the utilisation of artificial insemination and the increased number of foals per sire. A greater number of foals for a sire increases the probability to produce horses of sufficient quality for breeders to breed with, encouraging breeders to breed earlier. Dubois and Ricard (2007) confirmed that a higher number of foals per sire should decrease the generation interval.

With the increasing focus on Young Horse trials, the German breeder is encouraged to see the potential in a stallion earlier, not needing to wait for normal competition results or even progeny competition results before seeing the marketability of a stallion. Young stallions who win their performance test or perform well at Young Horse competitions like the DKB-Bundeschampionate are likely to encourage interest from a variety of breeders because of this early success and the resulting marketability of the stallions and their progeny.

2.8 Heritability

Heritability is defined as the proportion of phenotypic variation (V_P) that is due to variation in genetic values (V_G) (Wray and Visscher, 2008).

Equation 1:

$$H^2 = V_G/V_P$$

Where:

H = Heritability

V_P = Phenotypic variation

V_G = Genotypic variation

Lonka and Vainikainen, in 1946 were reportedly the first authors to publish heritability coefficients for horses (Varo, 1965). Within the literature, authors have focused on estimating variance components from two distinct measure of performance; data from the central station performance tests and from competition results.

2.8.1 Heritability of station performance test

Station performance testing generates a wealth of data and has been the focus of a number of studies estimating variance components (Bruns and Schade, 1998; Christmann et al., 1995; Gerber Olsson, et al., 2000; Hellsten, 2006; Huizinga, 1990; Huizinga et al., 1991).

Huizinga et al., (1991) used data from 1978 – 1988, collected from 337 three year old stallions. Their study illustrated heritability estimates as 0.64 for gaits and riding ability, 0.41 for cross country and 0.31 for jumping. Due to the highly standardised environmental conditions, estimates of heritability for performance traits are high and within the literature there are positive phenotypic and genetic correlations for most parameters (Olsson and Philipsson, 1992).

2.8.2 Heritability of competition performance

Irrespective of country or sub-population of Warmblood Sport Horse, the heritability of competition data has been reportedly lower than that of Station performance tests.

Huizinga et al., (1989), utilised a database of Dutch Warmblood horses that consisted of 6899 jumping horses and 10408 dressage horses, sired by 205 and 237 stallions, respectively. They found estimates for heritability for jumping to be 0.20 and dressage to be 0.10. Phenotypic and genetic correlations between performances at four, five and six years average 0.95 and 0.75, respectively. Koenen et al., (1995), used a population size of 3476 individual dressage horses and 3220 individual jumping horses and obtained estimated heritabilities for dressage and show-jumping of 0.17± 0.05 and 0.19 ± 0.04, respectively. Stewart et. al., (2010) calculated a similar value for the the heritability of dressage competition with dressage horses in the United Kingdom (0.15 ± 0.018). In a later study, Ducro et al., (2007), determined heritability values of 0.14 for both dressage and showjumping for studbook recorded free-jumping, movement related traits and competition.

2.9 Genetic correlation

The genetic correlation is an estimate of the additive genetic effect between traits.This is commonly represented by a numerical value. A value above that of zero signifies that traits are influenced by similar genes (Lynch and Walsh, 1998).

The station tests conducted on individuals provides genetic correlation values for comparison to that of the individuals performance. This is a good indicator of performance as a result of genetic influences in individuals involved in different breeding programmes.

Generally genetic correlation between station performance testing and observations in competition data has been high (0.70 to 0.90), with heritability also high (0.40 to 0.60) (Ricard *et al,.* 2000).

A study of the first stallion inspection traits with dressage and showjumping performance conducted by Ducro *et al.,* (2007) indicated that the genetic correlation between free jumping traits and show-jumping was all above 0.52, with four traits having estimates above 080. Predictably, genetic correlations of free jumping

Ducro, et al., (2007) also illustrated that the traits of conformation and movement showed a high correlation to performance in dressage horses (around a value of 0.68), but only moderate correlation to performance in show-jumping (a value of approximately 0.26).

Likewise, Gelinder et al., (2001) conducted a study involving the Swedish Warmblood population, which illustrated that the genetic correlations between jumping traits in stallion performance tests and jumping at competitions (0.74 to 0.88) were higher than correlations between gaits in Stallion Performance Tests and dressage at competitions (0.20 to 0.66).

In a study of eventing horse competitons, Ricard and Chany (2001) found that the genetic correlations of eventing with jumping and dressage performance was 0.45, and 0.58 respectively.

2.10 Inbreeding: Advantages and disadvantages

Interest in scientific research relating to inbreeding and performance in horses has been documented from at least the early part of the 20th century (Pearson and Lush, 1993). Many horse breeders advocate the use of inbreeding (Azevedo and Barata, 1982; Bohlin and

Ronningen, 1975; Rasmussen and Faversham, 1999; Potočnik et al., 2009; Borowska and Szwaczkowski, 1975; Radomska et al., 1984; G. Rozhdestvenskaya, 1972).

The use of Inbreeding in a population is often focused on the selection of desirable genes with the intention of increasing the frequency of said genes (Fisher, 1965). A negative factor would be the result of a loss of heterosis in a population with fixed genes expressed and an increased risk of recessive defects expressed (Ercanbrack and Knight, 1991; Frankel, 1981).

The consequences of inbreeding are manifested in terms of inbreeding depression, causing a depression of performance (Klemetsdal, 1998) an increase in undesirable recessive disorders, and a loss in genetic variation (Kearney, 2004). Koenen and van Veldhuizen (1995), Uimari and Kennedy (1990) and de Boer and van Arendonk (1992), all indicated a regression in performance in relation to the inbreeding coefficient.

Lande (1995), suggests that inbreeding depression is mainly due to a limited number of recessive mutations. By implication, selection may then rid the population of some of its mutational load (Falconer, 1960).

In studies involving the Holstein Dairy Cow population, Miglior and Burnside (1995), used Models consisting of a linear regression of performance on inbreeding with an additive genetic effect, including and excluding the dominance genetic. From this, it was determined that an inclination towards increased inbreeding depression was obtained from the simpler of the models in each of the studies. Hence, it was recommended that one could utilise a simple model to quantify the relationship of inbreeding and decreased production .

Frankham et al., (1993), also argues that selection is able to counteract a significant part of inbreeding depression over time. Likewise, Falconer (1960) and Fikse (1997) both stress that the problem with the estimation of inbreeding depression is the effect of selection. This is specifically relevant to Warmblood analysis as Warmblood breeding heavily utilises phenotypic selection.

2.10.1 Inbreeding in relevant horse populations

The inbreeding observed in equine studbooks reflects the breeding structure (open or closed studbook), the size of the studbook and the length of time that the studbook has been in existence.

In the closed studbook of the Andalusian breed, it was reported that the average inbreeding coefficient was 8.48 (Valera et al. 2005).

An even greater inbreeding coefficient has been reported for the closed Friesian breed as they underwent a significant population bottleneck in the early 1900's with only 3 breeding stallions and 34 mares. Compounding this effect was another bottleneck in the 1960's as a result of the advent of mechanisation on European farms. The mare population declined to as little as 500 mares (Dijkstra, 1996). Sevinga, et al., (2004) estimated an inbreeding coefficient of ± 15.7 in Friesian horse population.

In another closed studbook, despite no documented reports of population bottlenecks, the Norwegian Cold blooded trotter has an average inbreeding coefficient of 7.5 (Klemetsdal, 1998).

Inbreeding is especially pertinent to the Thoroughbred horse (Cunningham, 1991; Field and Cunnimgham, 1976; Gillespie, 1971; Pern, 1972; Langlois, 1980; Thiruvenkadan et al. 2009) as it is one of the most inbred breeds in the world concerning base genetic material (Klemetsdal, 1992) and as a closed studbook, it forms a substantial genetic base for the modern Warmblood horse. Ten founder female horses account for 72% of maternal lineages, while one founder stallion is responsible for 95%of paternal lineages (Cunningham et al. 2001). Four stallions account for a third of the genes and a total of 21 horses account for 80% of the makeup of the modern population (Cunningham, 1991). Castle (2007) studied Thoroughbreds in Australia, and determined the inbreeding coefficient to be 14.33.

As the Thoroughbred breed operates with a closed studbook (Castle, 2007), inbreeding can only increase and there is therefore an inevitable risk of inbreeding depression in the breed.

Federico Tesio (1869-1954) is considered in Thoroughbred circles as the 'father of inbreeding lore' (Rasmussen and Faversham, 1999). Reputedly using a principle of inbreeding, he won twenty-four Italian derby races (Tesio, 1947). His focus was on obtaining the appropriate sex balance in his inbreeding models. Following from Tesio's work, Rasmussen and Faversham (1999) devised a system of categorising inbreeding and coined the phrase the "Rasmussen Factor", which indicated a certain level of inbreeding. They claimed that the Rasmussen Factor (RF) occurred 50% more often among the top class runners than it did in the general population. However, Lyons (2001) disputed Rasmussen's findings, and concluded that, in general, the higher-class runners descend from a narrower range of breeding stock than the population at large.

With this high level of inbreeding, the effect of inbreeding depression seems obvious; the Thoroughbred shows a foaling rate of only 50% (Bailey, 1998) and their racing performance, as measured by the winning times of horses since 1910, have been static (Hill, 1998), despite intensive selection for performance (Cunningham, 1991; Hill, 1998; Langlois, 1980). This indicates that the limited effective population size and intense selection may have led to a plateau in performance, hence the apparent heritability of performance is illusory. Gaffney and Cunningham (1988), tested the explanation that additive genetic variance in performance may have been exhausted in terms of strong selection by estimating the genetic trend in performance over the time period 1952 to 1977 by using TIMEFORM handicap ratings and expressed racing merit as a weight in pounds as per their handicap. They indicate that their results show that a lack of improving race times is not due to insufficient genetic variance in the Thoroughbred racing population.

A wild horse population possibly demonstrates the ideal structure of a closed horse population study. However, inbreeding coefficients are generally lower than expected due to random mating (Berger and Cunningham, 1987; Duncan et al. 1984), illustrating that nature itself has an inherent restrictive mechanism protecting against the effect of inbreeding depression.

In the closed equine studbooks, the inbreeding coefficient reported is generally higher than in the open studbooks of the Warmblood horse.

The Hanoverian and the majority of other Warmblood breed types operate as an open studbook system (Bruns and Christmann, 1995; Niemann, 2009) and by definition would migrate towards an outcrossed horse with a relatively low inbreeding coefficient .

During the 1980's, the Hanoverian population had an inbreeding co-efficient of 1.2% and in 2006 it was 1.4% (Niemann, 2009). Hamann and Distl (2008), analysed a set of 310,109 Hanoverian horses and established the mean coefficient of inbreeding was 1.33%, 1.19%, and 1.29% for the reference population (all Hanoverian horses born between 1980 and 1995), stallions, and breeding mares, respectively.

Also an example of an open breed book and representative of a more diverse range, a 2011 study found inbreeding coefficients in the Polish Warmblood that ranged from 0.01 to 25 (Borowska et al., 2011). However, this is perhaps a misleading statistic with 93,59 % of the population without inbreeding and only 0.05 % of the population with an inbreeding coefficient of 25 (only 4 horses in a population of 8512).

As could be expected in a recent breed type, the Spanish Sport Horse, having been founded in 2002, is reported to have an inbreeding coefficient of 0.66% (Bartolome, 2011).

An open studbook structure with a relatively small effective breed size is the Dutch Harness Horse. Schurink's (2012) study indicates they had an average inbreeding coefficient of 5.3.

Inbreeding in the Selle Francais (SF) breed group is well established as shown by Dubois (Dubois and Ricard, 2007). This study showed a steady increase in the inbreeding coefficient from 1974 to 2002, with 100% of the 2,002 horses classified as inbred, with an average inbreeding coefficient of 1.4 (*Figure* 2). However, this remains a low figure and so is unlikely that it would result in any significant phenotypic trait.

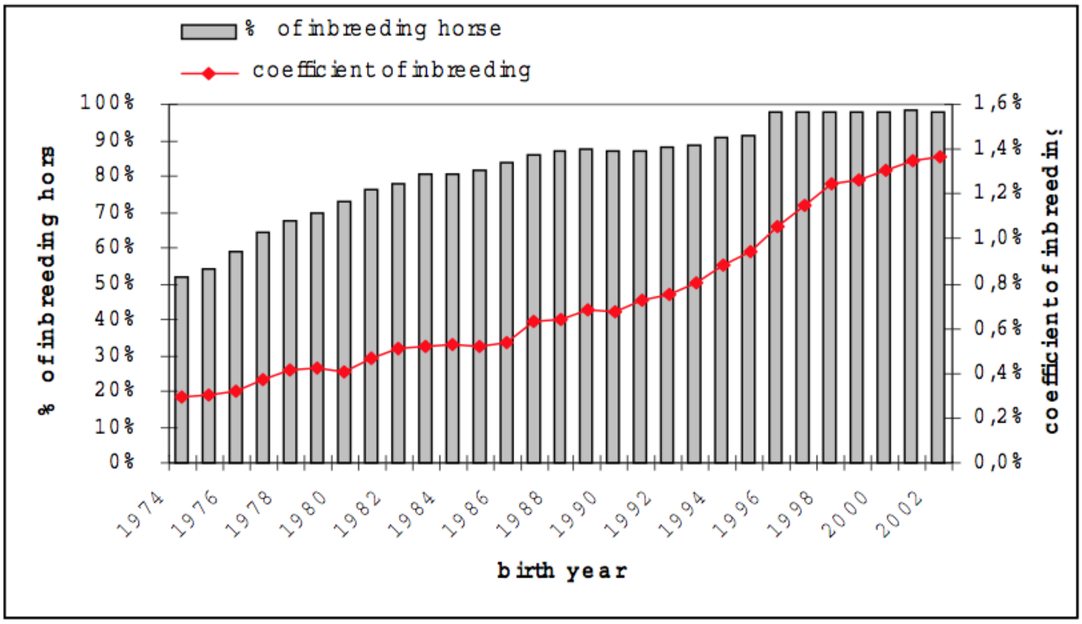

Figure 2. Bar graph with corresponding line regression illustrating the relationship between years in which horses were born, the percentage (%) of inbreeding and coefficient of inbreeding in Selle Francais Warmblood horse populations from the year 1974 to 2002. The bar graphs indicate the correlation between birth year and percentage (%) of inbreeding. The line regression (—◆—) represents the correlation between birth year and the coefficient of inbreeding.

Table 1. Collates reported figures on IBC for specific breeds, and their authors.

Breed	Reported IBC (±)	Author
Spanish Sport Horse	0.0066	(Bartolome, 2011)
hanoverian	1.4	(Niemann, 2009)
Selle Francais	1.4	(Dubois and Ricard, 2007)
Dutch harness horse	5.3	(Schurink, 2012)
Norwegian Cold blooded trotter	7.5	(Bjørnstad et al, 2000)
Andalusian breed	8.48	(Valera et al. 2005)
Thoroughbred (Australia)	14.33	(Castle, 2007)
Friesian	15.7	(Sevinga, et al. 2004)
Polish Warmblood	0.01 - 25	(Borowska et al. 2011)

2.10.2 A relevant threshold of inbreeding

While Ducro et al. (2006), alludes to a critical level of inbreeding with relation to performance of 1%, the understanding of "critical levels" in relevant populations is still poorly understood (Edmands, 2007) and more research needs to be conducted.

2.10.3 Calculating Inbreeding

Various Algorithms have been developed for methods to select and mate animals to minimise the conditioned response on effective population size or rate of inbreeding (Brisbane and Gibson, 1995; Caballero and Santiago, 1996; Woolliams, 1998).

Geneticists have used several different measures to rank genetic closeness. The most commonly used one is the coefficient of inbreeding (F) defined by Sewall Wright in the early 1920s (Wright, 1921).

Equation 2:

$$F_X = \sum \left[\left(\frac{1}{2} \right)^{n_1 + n_2 + 1} (1 + F_A) \right]$$

F_X = Inbreeding Coefficient of individual horse

F_A = Inbreeding Coefficient of the common ancestor

n_1 = Number of generations from the sire to the common ancestor

n_2 = Number of generations from the dam to the common ancestor

Wright (1922) illustrated how F (referring to inbreeding coefficient) can be calculated, however, his method of trajectories is unstructured when packaged into a program.

Two programs are commonly used to compute inbreeding coefficients of individuals in a population:

The Meuwissen method (Meuw.f) (Meuwissen and Luo, 1992) method is a modification of the method determined by Quaas (1976). This approach uses the Cholesky factor (Quaas, 1976) of the relationship matrix, wherein each row of this factor is built by tracing the entire pedigree of each individual. The inbreeding coefficient is then obtained from the elements of this row, including the inbreeding coefficients of the ancestors. This method is ideal for pedigrees consisting of less than 15 generations.

Van Raden's method (*vanrad.f*) (van Raden, 1992) is derived from a tabular method. It relies on building the relationship matrix of each individual and of its subsequent ancestors. The inbreeding coefficients of all these animals are then deducted from the diagonal elements of this matrix. This process is laborious and slow but is extremely accurate, thus has the ability to distinguish close from far inbreeding and also makes it possible to distinguish inbred or related founders. This is very useful when the pedigree information is heterogeneous.

2.10.3.1 Pedigree completeness

When calculating the inbreeding coefficient of an individual or the average inbreeding coefficient of a population, the completeness of pedigree has a large effect on the outcome of the calculation (Cothran, 1984), hence estimates of inbreeding depression are least accurate when based on performance data of animals with incomplete pedigrees (Fikse et al., 1997).

2.11 Inbreeding and performance.

A limited, but interesting array of studies have been undertaken in inbreeding and performance in the equine athlete.

Klemetsdal (1998), studied the relationship between racing performance and inbreeding in the Norwegian Cold Blooded Trotter, utilising a database of horses born from 1972 until 1986. A total of 7,897 out of 12,569 horses within this group had all ancestors known for five generations, which resulted in a dataset of 244,807 records. The study indicated that racing performance in the Norwegian cold blood trotter was depressed in relation to inbreeding. Performance was measured by accumulated, transformed and standardized earnings (ATSE). The average inbreeding coefficient in the population was around 7.5%. The animals that were inbred to 15% had a fourfold reduction in performance amounting to 0.145 phenotypic standard deviations.

An important point is that the effects of Inbreeding depression are not the same across different equine breeds or types.

In the former USSR, a number of studies have compared the phenotypic performance of inbred animals compared to that of outbred animals in both the Orlov trotter and the Thoroughbred. A lower level of performance associated with inbreeding was seen in most studies (Afanasjev, 1965; Fomin, 1983; Odnoletkova, 1998; Pern, 1973: Rozhdestvenskaya, 1978). Rozhdestvenskaya (1972) however, found a lack of effect of inbreeding depression on Racing Performance was illustrated. These studies dealt with relatively low population numbers, and as such must be viewed in context. The number of animals in the inbred/outbred groupings was; 755/1 587 for Rozhdestvenskaya's (1978) study, 1 290/721 for Pern's (1973) and 1176/148 for Fomin's. Afansjev (1965) used 606 horses in his study, while Odnoletkova (1998) did not mention the numbers of horses studied.

Inbreeding depression is not only measured in terms of "competition" performance, but also has been associated with reproductive capability and musculoskeletal health.

Cothran (1984), showed the relationship between inbreeding and reproductive performance was not consistent between trotters and pacers. For trotters (F = 10.3), there was a trend for an increase in conception and foaling rates with increased inbreeding. This contrasted with the results for pacers (F = 7.4), which showed a decrease in reproductive performance with increased inbreeding. Cothran (1984), therefore concluded that inbreeding was not a significant factor in the reproductive performance of standardbred horses.

Van Eldik et al., (2006) conducted a study of the relationship between inbreeding and semen quality examined in 285 Shetland pony stallions. The coefficients of inbreeding ranged from 0 to 25% (mean S.D.: 3 ± 4.6%). The stallions were divided into six inbreeding classes (0–1, 1–2, 2–5, 5–8, 8–12 and >12%) containing 132, 40, 42, 27, 25 and 19 animals, respectively. Based on a standard examination of two ejaculates collected at a 1.5 to 3 hour interval, the degree of inbreeding significantly affected many aspects of sperm production and quality. Specifically, coefficients of inbreeding above 2% were associated with lower percentages of motility ($p<0.01$) and observed morphologically normal sperm ($p<0.001$).

Performance can also be measured in terms of “production traits” and as there is a certain amount of crossover in terms of genetic relevance, other animal species should be observed.

In a study to determine the effect of inbreeding on milk production, Thompson and Everett (2000), calculated that milk production losses per lactation caused by inbreeding were generally 35 kg per percentage inbreeding level greater than F = 1 but increased to 55 kg per percentage inbreeding level from F = 7 to F = 10. In their study of lifetime performance of Dairy Cattle, Smith and Casell (1998), indicated that inbreeding decreased the mature equivalent production of milk, fat, and protein during first lactation by 27, 0.9, and 0.8 kg and the lifetime production of milk, fat, and protein by 177, 6.0, and 5.5 kg, respectively, per 1% increase in inbreeding.

Studies involving sheep have also showed an unfavourable relation between production traits (such as wool production) and inbreeding depression. Ercanbrack and Knight (1991), used Rambouillet, Targhee and Columbia ewes to calculate the effects on fleece weight, which were curvilinear and amounted to reductions of 0.35 kg for Rambouillet, 0.18kg for Targhee and 0 kg for Columbia sheep at levels of inbreeding approaching F = 20; however, Columbia fleece weights declined rapidly at levels exceeding F = 20 for ewes. The average economic loss per ewe in value of production was estimated at $17 for inbreeding below F = 20 and as high as $36 for inbreeding approaching F = 20.

Chapter 3 Literature Summary

The focus of most Sport Horse breed Societies is competition and to improve performance in both jumping and dressage by following distinct breeding objectives and selecting for clearly defined genotypic and phenotypic traits (Koenen and Alridge, 2004).

The measurement of performance in the Sport Horse has been extensively refined since the initiation of most modern breed societies. Various methods of measuring performance have been utilised, including; annual earnings (Hintz, 1980), competition results (Aldridge et al. 2000), the use of centralised performance tests involving numerical scores (Dorofejew and Dorofejewa, 1976), progeny analysis (Christmann et al. 1995) and pedigree analysis (Field and Cunnimgham, 1976). The most integrated measure of performance used in Germany is the iEBV (Integrated Breed Value Estimation) (Lührs-Behnke and Kalm, 2002; Schöpke et al. 2013). The iEBV utilises performance information from both breeding and sport aspects. This includes; sport events, Young Horse competitions, performance tests of mares and stallions and lineage data. All breeding values are standardised to a relative value having a mean of 100 and a standard deviation of 20 points (VIT, 2016).

Interest in scientific research relating inbreeding and performance in horses has been documented from at least the early part of the 20th century (Pearson and Lush, 1933). One of the most interesting papers in relation to this study is that by Klemetsdal (1998). Klemetsdal (1998) found that racing performance in the Norwegian cold blood trotter was depressed in relation to inbreeding and that animals that were inbred to 15% had a fourfold reduction in performance, amounting to 0.145 phenotypic standard deviations.

A number of European horse populations exist with high average inbreeding coefficients. (Borowska et al. 2011; Schurink etal. 2012; Sevinga et al. 2004; Valera et al. 2005), while inbreeding is prevalent in most Sport Horse breeds (Bartolome et al. 2011; Borowska et al. 2011; Bruns and Christmann, 1995; Dubois and Ricard, 2007; Hamann and Distl, 2008; Niemann B, 2009; Schurink et al. 2012).

Artificial insemination has revolutionised the Sport Horse breeding, with the risk in terms of inbreeding being that many more mares from all over the world have access to the same top stallions, in effect reducing the pool of stallions used and thereby restricting the gene pool (Niemann B, 2009). To balance this, most Sport Horse organisations run an open stud book, and top stallions from outside genetic sources are often used to infuse new genetic material into the breed types (Koenen et al., 2004).

Most Sport Horse societies utilise the Thoroughbred horse within their breeeding programs. This has special relevance in that inbreeding is especially prevalent in the Thoroughbred, where four founding stallions account for a third of the genes and a total of 21 horses account for 80% of the modern population (Cunningham, 1991).

With such ubiquity of inbreeding in equine breeds, the relationship between inbreeding (and subsequently inbreeding depression) and performance must be explored with relevant critical levels of inbreeding established. To date, there is little research establishing such levels.

The most extensive evaluation model for studies relating the correlation of inbreeding to performance, that utilizes a multitrait system to allow for standardization of traits, both genetic and environmental and from a variety of sources, is the BLUP (Best Linear Unbiased Prediction) Multitrait Repeatability Animal Model (van Vleck, 1998). The model allows for relationships to all relatives and performance records of related horses, while also allowing for confounding environmental influences.

For the calculation of the inbreeding coefficients, two methods are commonly used: the Meuwissen method (Meuwissen and Luo, 1992) and the van Raden method (van Raden, 1992). The Meuwissen method uses the Cholesky factor of relationship matrix where each row is built by tracing the entire pedigree of each individual. The van Raden's method is more complex and is derived from a tabular method that builds a relationship matrix for each of the individuals and for each subsequent ancestor.

Chapter 4 The hypothesis

The hypothesis to be tested in this thesis is;

"There will be a significant positive linear relationship of the inbreeding coefficient (IBC) with the intergrated breeding value (iEBV) as a measure of performance, in the 2012 population of Hanoverian Sport Horses born between 1990 and 2009."

Chapter 5 Materials and method

5.1 Dataset and Range

There were 642,862 potential horses with iEBV's calculated in the 2012 integrated Genetic Evaluation (IGE 2012) of the German Vereinigte Informationssysteme Tierhaltung w.V. This dataset was refined to 84,724 horses by using the criteria for a registered Hanoverian born between the years 1990 and 2009.

Of the 84,724 horses that fulfilled the selection criteria, 78,907 were horses with their own performance records which were used in the genetic evaluation. Of these, 50,408 horses all had their own performance records and had both a Hanoverian Sire and Dam.

5.2 Pedigree completeness

A major factor in the determination of the inbreeding coefficient is the completeness of pedigree. The more complete and greater the number of generations used, the more accurate the inbreeding coefficient (Klemetsdal, 1998; Meuwissen and Luo, 1992).

Table 2 refers to the accuracy of the pedigree information in the Hanoverian dataset used.

The pedigree of the horses were traced back as far as possible with a total number of horses N=168 098. The maximum number of ancestral generations was 37.

Table 2. Pedigree completeness over the first 20 ancestral generations in a sample of N=84,724 Hanoverian Warmblood horses born 1990-2009, with average completeness of parent information (1.00 = sire and dam known, 0.50 = sire or dam known, 0.00 = both parents unknown).

Generation	Number of horses within the generation	Average completeness of pedigree information
0	84,724	1.00
1	36,206	1.00
2	27,528	1.00
3	24,426	0.99
4	24,110	0.96
5	24,940	0.89
6	24,891	0.81
7	23,369	0.76
8	20,910	0.72
9	17,815	0.68
10	14,502	0.66
11	11,458	0.65
12	8,970	0.63
13	6,932	0.62
14	5,384	0.61
15	4,189	0.60
16	3,324	0.58
17	2,621	0.57
18	2,125	0.56

19	1,710	0.54
20	1,352	0.51

As shown in *Table 2* The pedigree records up to the grandparent generation is 100% accurate and it is only after the 6th generation that we see a noticeable decrease in pedigree information (less than 80%).

5.3 Inbreeding

For computation of inbreeding coefficients, two methods were used; the Meuwissen method (Meuwissen and Luo, 1992) and the van Raden method (van Raden, 1992). The software package PEDIG was used for both methods.

PEDIG is a fortran 77 software package (Boichard, 2002) which uses two computer programs (*Meuw.f* and *vanrad.f*) to output both the laborious van Raden method (van Raden, 1992) and the Meuwissen method (Meuwissen and Luo, 1992). It utilises several independent programs to calculate probabilities of gene origin of up to several tens of million individuals and so easily copes with the numbers of horses in the dataset.

For model 2 in this study, the horses were cataogorised according to their level of inbreeding; IBC=0.00, 0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, 0.05<IBC.

IBC was tested both as linear covariate (LC) or (in classes) as fixed effect (FE) and

The Inbreeding Coefficient was analysed for a significant difference between year groups (year of birth) and between sexes (sire and dam).

5.4 Performance

The 2012 Integrated Estimated Breeding Value (iEBV) was used as the quantitative measure of the horse's performance and was extracted from data collected and processed by the Vereinigte Informationssysteme Tierhaltung w.V. The iEBV's were calculated annually on behalf of the Fédération Equestre Nationale (FN), the national body responsible for the organisation of equestrian sport in Germany.

iEBV data were extracted for all 84,724 horses in the study.

The iEBV utilises performance information from both breeding and sport aspects. These were classified as follows;

1. Sport events - show jumping and dressage competitions (TSP) recorded by TORIS (Turnier ORganisations und Informations System) from 1995 onwards were considered. Each specific event was related to its level of competition e.g. an international event was weighted heavier than a national event.

2. Young Horses' show jumping and dressage competitions (ABP) were utilised. Competitions from 1995 onwards were recorded with TORIS and were processed for the evaluation.

3. Own performance test of mares (ZSP), as conducted by the various German breeding associations (from 1986 on), were included.

4. The Station Performance testing for young stallions was included (SPT). The traits considered were: score for walk, trot, canter, rideability and free jumping (score 1-10). The traits were calculated as the average of scores in training and final test.

All breeding values, as well as, part and total indices were standardised to a relative breeding value having a mean of 100 and a standard deviation of 20 points (genetic standard deviation) (VIT, 2016). Standardising breeding values made them interpretable and comparable as a consistent reference to the true genetic variation. Original breeding values were not publicised and were not available for this study.

Results were structured according to jumping and dressage traits, sex and birth year, in performance groupings of:

- All horses
- Horses with own performance
- Horses with own and offspring performance

5.6 Dressage vs Jumping in the iEBV

In the calculation of the iEBV, each horse was given values for dressage and jumping, respectively. (VIT, 2016).

5.7 Performance Publication

Estimated breeding values were published for public record for stallions only, and only if the estimated total index of jumping and dressage was at least 70% and if there were in total at least 5 offspring who had their own performance in the respective jumping and dressage areas.

5.8 Analysis

5.8.1 BLUP Analysis

The Evaluation was carried out using the BLUP (Best Linear Unbiased Prediction) Multitrait Repeatability Animal Model.

The analysis utilised a multitrait system and all traits, environmental and genetic, were analysed simultaneously with the use of different sources and connected via genetic standardised correlation. All Affects, environmental as well as genetic (testing, performance results and pedigree information), were directly corrected for each other, and so pre-adjustments were redundant.

The model took into account all known relationships between relatives and all information about performances of related horses. A horse (even without a performance record) achieved a score based on the relationship to all other relatives and further, their relationships and performance records.

With reference to this study, the model was simultaneously adjusted for biases, such as; age, sex and discipline. The BLUP analysis also allowed environmental factors, such as the relation to a professional or amateur rider and that rider's influence and performance on other such animals in the analysis. The repeatability of performance of horses and horse and rider combinations were allowed in the analysis. *Table 3* refers to the genetic parameters therein.

Table 3. Traits correlating for both jumping and dressage horses, including the different criteria. The diagonal values represent heritabilities and the proximal values indicate genetic correlations. TSP: (Turniersportprüfung) Sport events - show jumping and dressage competitions, APB: (Aufbauprüfung) Sport events – show jumping and dressage of Young Horses' competitions, ZSP: (Zuchtstutenprüfung) Own performance test of mares, VA: (Veranlagungsprüfung) ability test of young stallions, HLP: (Hengstleistungsprüfung) Own performance test of stallions.

	Trait		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
TSP	Jumping	1	0.04	0.14	0.63	0.13	0.14	0.10	0.23	0.19	0.26	-0.08	0.03	0.10	0.11	0.38	0.44
	Dressage	2		0.08	0.14	0.61	0.51	0.52	0.48	0.64	0.01	0.54	0.61	0.57	0.67	-0.03	0.09
ABP	Jumping	3			0.13	0.26	0.07	0.15	0.31	0.27	0.42	0.07	0.11	0.28	0.26	0.46	0.69
	Dressage	4				0.17	0.54	0.60	0.57	0.66	0.10	0.54	0.63	0.64	0.69	0.07	0.25
ZSP / VA	Walk	5					0.30	0.55	0.52	0.56	0.10	0.73	0.57	0.62	0.53	-0.04	0.04
	Trot	6						0.40	0.69	0.67	0.18	0.55	0.79	0.67	0.64	0.04	0.11
	Canter	7							0.37	0.67	0.25	0.49	0.60	0.73	0.59	0.15	0.30
	Rideability	8								0.32	0.17	0.57	0.68	0.72	0.77	0.02	0.18
	Free jumping	9									0.34	-0.08	0.04	0.12	0.06	0.87	0.77
HLP	Walk	10										0.37	0.65	0.62	0.58	-0.13	0.03
	Trot	11											0.52	0.74	0.75	-0.05	0.03
	Canter	12												0.44	0.72	0.17	0.29
	Rideability	13													0.42	0.04	0.19
	Free jumping	14														0.41	0.86
	Parc. jumping	15															0.34

5.8.2 Combination of traits and weighting for the iEBV calculation

The aim of the evaluation was to obtain an average value for the genetic disposition for jumping and dressage horses based on performance and testing results. Each horse received a breeding value for each trait. All traits were combined to provide a total index for dressage and jumping, respectively. Each trait was weighted according to its importance in the breeding scheme structure (see *Table 4*).

Table 4. Traits of both jumping and dressage horses used in the breeding value (iEBV) and the weighted value for each trait. Said traits also relate to the specific criteria used in calculating breeding values. TSP: (Turniersportprüfung) Sport events - show jumping and dressage competitions, APB: (Aufbauprüfung) Sport events – show jumping and dressage of Young Horses' competitions, ZSP: (Zuchtstutenprüfung) Own performance test of mares, VA: (Veranlagungsprüfung) ability test of young stallions, HLP: (Hengstleistungsprüfung) Own performance test of stallions.

		Dressage					Jumping				
		Part index				Total Index	Part index				Total Index
		TSP	ABP	ZSP/VA	HLP		TSP	ABP	ZSP/VA	HLP	
TSP	Jumping						1			0.25	0.25
	Dressage	1				0.25					
ABP	Jumping		1					1		0.25	0.25
	Dressage					0.25					
ZSP/VA	Walk			0.25		0.0625					
	Trot			0.25		0.0625					
	Canter			0.25		0.0625					
	Rideability			0.25		0.0625					
	Free Jumping									1	0.25
HLP	Walk				0.25	0.0625					
	Trot				0.25	0.0625					
	Canter				0.25	0.0625					
	Rideability				0.25	0.0625					
	Free Jumping									0.5	0.125
	Jumping with rider									0.5	0.125

5.8.3 Statistical methods describing the relationship between inbreeding (IBC) and genetic performance potential (iEBV)

A regression model was fitted to relate inbreeding measured by the Meuwissen method (Meuwissen and Luo, 1992) and the van Raden method (van Raden, 1992) to individual performance (using the 2012 published Integrated Breeding Value (iEBV). Statistical analyses were performed using the software package SAS (Statistical Analyses System), version 9.2. Basic procedures MEANS and FREQ for the descriptive analyses were calculated, along with the procedure GLM for the analyses of variance, involving the confounding factors of year, sex and discipline (jumping or dressage).

The relationship of inbreeding and performance was tested using two different linear models.

In the first model, inbreeding was included as a continuous variable. In the second model, inbreeding was divided into categories with 5 various levels of inbreeding.

Model 1:

$y_{ijkl} = \mu + b\ IBCi + SEXj + BYEARk + eijkl$

y_{ijkl} = breeding value (iEBV)

μ = model constant

IBCi = inbreeding coefficient of $horse_i$

SEXj = fixed effect of sex (j=1-2; stallions, mares)

$BYEAR_k$ = fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008-2009)

eijkl = random residual

Model 2:

$y_{ijkl} = \mu + IBCCi + SEXj + BYEARk + eijkl$

$y_{ijk}l$ = breeding value (iEBV)

μ = model constant

$IBCC_i$ = fixed effect of inbreeding coefficient class (i=1-5; IBC=0.00, $0.00 < IBC \leq 0.01$, $0.01 < IBC \leq 0.02$, $0.02 < IBC \leq 0.05$, $IBC > 0.05$)

SEX_j = fixed effect of sex (j=1-2; stallions, mares)

$BYEAR_k$ = fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008-2009)

$_{eijkl}$ = random residual

Chapter 6 Results

6.1 Inbreeding

The results were identical (100% fits) for both methods of calculating inbreeding coefficients (The Meuwissen method (Meuwissen and Luo, 1992) and the van Raden method (van Raden, 1992)), thus a single inbreeding coefficient was used for each animal.

There were very similar results for the mean inbreeding coefficient of all horses with own performance (N=78,907) and horses with Hanoverian parents (N=50,408) in the genetic evaluation. There were significant differences between birth year classes (p <0.001) for the least square means (LSM) estimates of inbreeding (*Figure 3*).

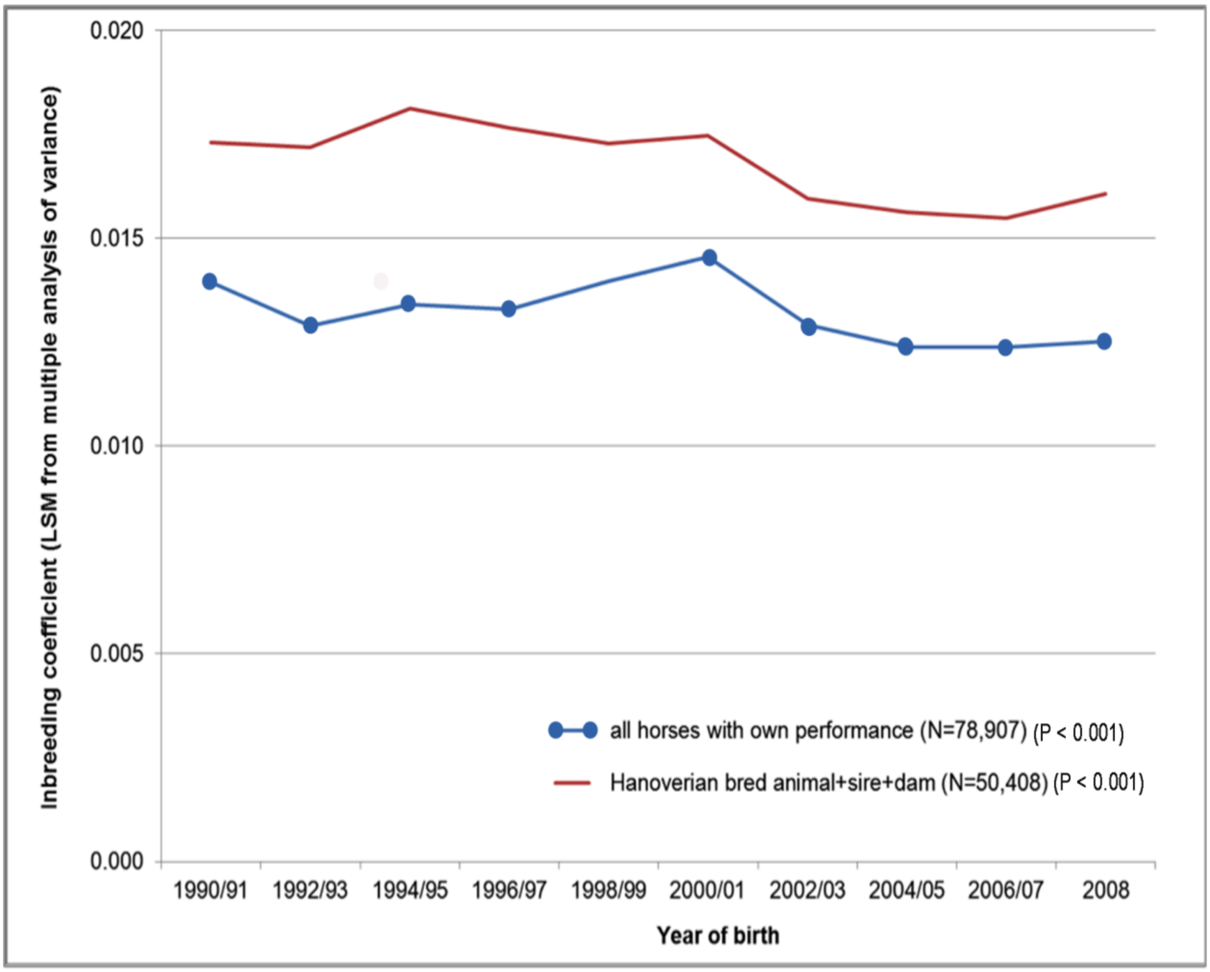

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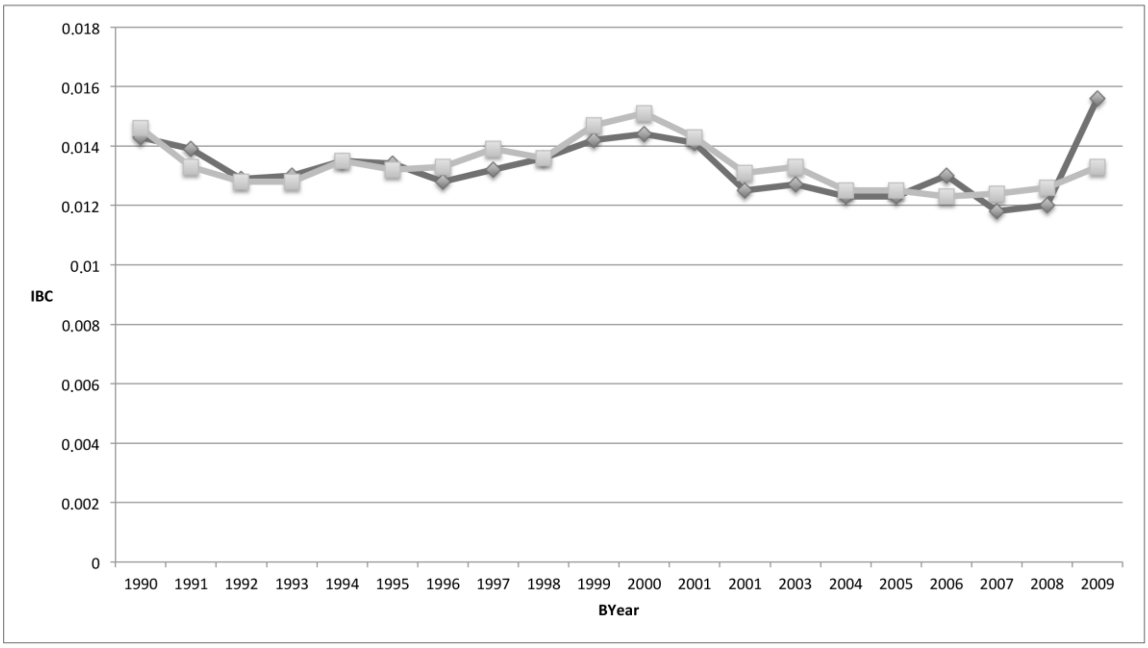
Figure 3. Graph of the the year of birth and the inbreeding coefficient (Least Square Mean). All horses with own performance (●—●) (N= 78.907) and the Hanoverian bred horses (—♦—) (N = 50.408).

Within the model, there was no significant effect of sex; sire (p=0.09) or dam (p=0.17). (*Figure 4*).



Light grey = IBC-female
Dark grey = IBC-male

Figure 4. Graph of IBC (inbreeding coefficient) and the birth years of male and female subgroups. This includes the IBC-M (male horses) as illustrated ( ) with a regression equation; y=-0.3642x+861.05 with a R^2 value of 0.05165 and the IBC-F (female horses) ( ) with regression equation; y=-0.5098x+1152.9 and R^2 value of 0.13798.

6.2 Relationship between Inbreeding and Performance (as measured by genetic performance potential)

6.2.1 Model 1

Tables 5 to 8 show the results of variance with inbreeding coefficients (IBC) as a linear covariate for various subgroups of horses ("Total horses" and "horses with own performance" for; TID, TIJ, TCD, TCJ, YCD, YCJ, MPTD, MPTJ, SPTD, SPTJ) with coefficients of determination (proportions of explained variance, R^2), error probabilities (P-value), and linear regression coefficient for IBC class.

The linear regression coefficient for the IBC (b) represents the linear relationship to iEBV . In dressage, this showed a significant (p<0.001) positive relationship in all categories (*Table 5 and Table 6*), while Jumping presented a significant (p<0.001) negative relationship in all categories. (*Table 7 and Table* 8).

Table. 5 Breedings value for "total dressage horses" in relation to the R^2 value and the linear regression coefficients for IBC (inbreeding coefficient) including the mean ± the standard error, along with the P-value. TID = Total Index Dressage, TCD = iEBV for Tournament competitions dressage, YCD = iEBV for Young Horse competitions dressage, MPTD = iEBV for dressage in mare performance test and SPTD = iEBV for dressage in stallion performance test.

Breeding Value	R^2	Linear regression coefficients for IBC	P-value
TID	0.228	48.54	<0.001
TCD	0.206	39.65	<0.001
YCD	0.241	24.27	<0.001
MPTD	0.231	43.46	<0.001
SPTD	0.210	57.52	<0.001

All subgroups of "Total Dressage horses" (TID, TCD, YCD, MPTD and SPTD) all showed an extremely significant (P<0.001) positive Linear regression relationship for IBC with a fairly tight distribution of R^2 from 0.206 – 0.241 (0.035) demonstrating a relative consistency across the data groups

Table 6. Breedings value for "dressage horses with own performance" in relation to the R^2 value and the linear regression coefficients for IBC (inbreeding coefficient) including the mean ± the standard error, along with the P-value. TID = Total Index Dressage, TCD = iEBV for Tournament competitions dressage, YCD = iEBV for Young Horse competitions dressage, MPTD = iEBV for dressage in mare performance test and SPTD = iEBV for dressage in stallion performance test.

Breeding Value	**R^2**	**Linear regression coefficients for IBC**	**P-value**
TID	0.224	49.70	<0.001
TCD	0.204	40.36	<0.001
YCD	0/237	25.01	<0.001
MPTD	0.227	44.26	<0.001
SPTD	0.205	59.07	<0.001

All subgroups of "Dressage horses with own performance" (TID, TCD, YCD, MPTD and SPTD) all showed an extremely significant (P<0.001) positive Linear regression relationship for IBC with a fairly tight distribution of R^2 from 0.204 – 0.237 (0.033) demonstrating a relative consistency across the data groups.

Table 7. Breeding values for "total jumping horses" in relation to the R^2 value and the linear regression coefficients for IBC (inbreeding coefficient) including the mean ± the standard error, along with the P-value. TIJ = Total Index Jumping, TCJ = iEBV for Tournament competitions jumping, YCJ = iEBV for Young Horse competitions jumping, MPTJ = iEBV for jumping in mare performance test and SPTJ = iEBV for jumping in stallion performance test.

Breeding Value	R^2	Linear regression coefficients for IBC	P-value
TIJ	0.065	-51.01	<0.001
TCJ	0.131	-64.79	<0.001
YCJ	0.138	-63.17	<0.001
MPTJ	0.026	-13.71	0.008
SPTJ	0.048	-40.32	<0.001

All subgroups of "Total Jumping horses" (TIJ, TCJ, YCJ, MPTJ and SPTJ) showed an extremely significant (P<0.001) negative Linear regression relationship for IBC with a fairly tight distribution of R^2 from 0.065 – 0.131 (0.066) demonstrating a relative consistency across the data groups, though not quite as condense as Dressage (0.035)

Table 8. Breeding values for jumping horses with own performance in relation to the R^2 value and the linear regression coefficients for IBC (inbreeding coefficient) including the mean ± the standard error, along with the P-value. TIJ = Total Index Jumping, TCJ = iEBV for Tournament competitions jumping, YCJ = iEBV for Young Horse competitions jumping, MPTJ = iEBV for jumping in mare performance test and SPTJ = iEBV for jumping in stallion performance test.

Breeding Value	R^2	Linear regression coefficients for IBC	P-value
TIJ	0.065	-54.67	<0.001
TCJ	0.135	-67.51	<0.001
YCJ	0.138	-65.79	<0.001
MPTJ	0.025	-16.91	0.002
SPTJ	0.048	-43.58	<0.001

All subgroups of "Jumping horses with own performance" (TIJ, TCJ, YCJ, MPTJ and SPTJ) all showed an extremely significant ($P < 0.001$) negative Linear regression relationship for IBC with a fairly tight distribution of R^2 from 0.065 – 0.138 (0.073) demonstrating a relative consistency across the data groups, though not quite as condense as Dressage (0.033). These show extremely consistent results to the group "All jumping horses".

Tables 5,6,7 and 8 show the coefficient of IBC total's for the four groups Dressage ("Total" and "with own performance") and Jumping ("Total" and "with own performance") are 48.54, 49.70, -51,01 and -54,67 with a complete range of 13.71. It can be seen that dressage has a positive linear regression relationship with the IBC, while jumping has a negative linear regression relationship. All subgroups within dressage and all subgroups within jumping show an extremely tight distribution of results, demonstrating the high degree of consistancy within the data and across all subgroups.

A linear regression coefficient of 48.54 was for the subgroup "Total Dressage horses" with total population size of N=84,724 (all horses) and a similar linear regression coefficient of 49.70 for the subgroup of "Dressage horses with own performance" (N=78,907) indicated a positive relationship between IBC and iEBV for dressage horses.

A linear regression coefficient of -51.01 was for the subgroup "Total Jumping horses" with total population size of N=84,724 (all horses) and a similar linear regression coefficient of -54.67 for the subgroup of "Jumping horses with own performance" (N=78,907) indicated a negative relationship between IBC and iEBV for Jumping horses.

The R^2 values for the models were moderate, though better R^2 were obtained for the dressage-related measures of performance than for the jumping-related. Across all models there was a linear association of inbreeding with the respective iEBV. Though in general the R^2 figures are not high, they are relatively constant and both models and all subgroups have a low error probability ($P<0.001$) indicating significant results.

6.2.1.1 relative effect of inbreeding – model 1

By establishing a relative linear coefficient for IBC in the formulae;

yijkl = μ + b IBCi + SEXj + BYEARk + eijkl

Where;

yijkl = breeding value (iEBV)

μ = model constant

IBCi = linear covariate of inbreeding coefficient with linear regression coefficient b

SEXj = fixed effect of sex (j=1-2; male, female)

BYEARk = fixed effect of birth year class (k=1-10; 1990-1991, 1992-1993, ..., 2008-2009)

eijkl = random residual

The relative influence of IBC can be determined and compared to the year cohort and sex of the horse.

Model 1 defines the contribution of inbreeding (IBC) to iEBV (where average iEBV = 100) is b(coefficient of IBC) * IBC (where the average inbreeding coefficient is 0.015).

Using the TID and TIJ figures from *Tables 5 - 8* ("Total" and "with own performance", the "contribution of inbreeding to iEBV (b IBCi)" values can therefore be calculated. (see *Table 9*).

i.e. for the group TID (N=84724) where b = 48.54 and average IBC = 0.015, the contribution of inbreeding to iEBV is b * IBC = 48.54 * 0.015 = 0.7281

The contribution of inbreeding to iEBV is then be summerised in *Table 9*.

Table 9. Coefficient of IBC for dressage and jumping horses (for horses with "Total" (N=84724) and "with own performance" (N=78907)) in relation to the average inbreeding level, the contribution of inbreeding to iEBV and the overall average iEBV. TID = Total Index Dressage, TIJ = Total Index Jumping.

b (Coefficient of IBC)	Average inbreeding level in horse (IBC)	contribution of inbreeding to iEBV (b IBCi)	average iEBV
TID, N=84724 All horses 48.54	0.015	0.7281	100
TID, N=78907 All horses with own performance 49.7	0.015	0.7455	100
TIJ, N=84724 All horses -51.01	0.015	0.76515	100
TIJ, N=78907 All horses with own performance -54.67	0.015	0.82005	100

Model 1 assesses the contribution of inbreeding to the iEBV of in the subgroup "All Dressage Horses" as 0.7281%. The contribution of inbreeding to the iEBV of in the subgroup "All Dressage

Horses with own performance" is 0.7455%. The contribution of inbreeding to the iEBV of in the subgroup "All jumping Horses" is 0.76515%. The contribution of inbreeding to the iEBV of in the subgroup "All Jumping Horses with own performance" is 0. 82005%

Despite the variation in IBC coefficient calculated from the different models, it is clear that the relative change in the measure of performance (iEBV) is negligible. As shown in *Table 9*, where the average horses in a given year of evaluation will have an iEBV of 100 and using the IBC coefficients calculated there is approximately 0.7% of the iEBV of all dressage horses that is attributed to the level of inbreeding. ,.

6.2.2 Model 2

Model 2 establishes the relative importance of the trait of inbreeding in influencing the iEBV as catagorized by IBC groupings.

Table 10. illustrates the distribution of horses across the various classes of inbreeding coefficient (IBC=0.00; 0<IBC≤0.01; 0.01<IBC≤0.02; 0.02<IBC≤0.05 IBC>0.05). The distribution shows a relatively even distribution with the majority of horses in the middle two groupings (0<IBC≤0.01 and 0.01<IBC≤0.02) and a small number of horses with either no IBC or above 0.05. (see appendix output file "db_inzk_zwintVB.2013.ZWINT.lst")

IBC class	**All horses** (N=84.724)	**Horses with own performance** (N=78.907)
IBC=0.00	1290	1170
0<IBC≤0.01	38778	36174
0.01<IBC≤0.02	28386	26457
0.02<IBC≤0.05	14721	13690
IBC>0.05	1549	1416

The majority of horses (67,164 horses, or 79%) of the horses are within the two IBC subgroups; 0<IBC≤0.01 and 0.01<IBC≤0.02. A relatively small proportion of only 15% (1290 horses) are without any inbreeding at all.

Tables 11 – 14 shows the results of multiple analyses of variance with inbreeding coefficient groupings for all horses (dressage and jumping respectively) and all horses with their own performance records (dressage and jumping respectively) catagorised in the groupings of normal competitions, Young Horse competitions, mare and stallion performance testing and total indices.

Table 11. Breeding values for all dressage horses in relation to the R^2 for each, over a variety of IBC classes and the subsequent P-value. TID = Total Index Dressage, TCD = iEBV for tournament competitions dressage, YCD = iEBV for Young Horse competitions dressage, MPTD = iEBV for dressage in mare performance test and stallion ability test and SPTD = iEBV for dressage in stallion performance test. Total population size is N=82714.

Breeding Value	R^2	IBC=0.00	0<IBC≤0.01	0.01<IBC≤0.02	0.02<IBC≤0.05	0.05<IBC	P-value
TID	0.229	93.50 ± 0.48	98.54 ± 0.09	98.81 ± 0.11	100.55 ± 0.14	98.55 ± 0.44	<0.001
TCD	0.208	94.85 ± 0.41	98.87 ± 0.08	99.19 ± 0.09	100.48 ± 0.12,	98.84 ± 0.37	<0.001
YCD	0.243	93.95 ± 0.39	98.05 ± 0.07	97.71 ± 0.09	99.00 ± 0.12,	97.58 ± 0.35	<0.001
MPTD	0.233	93.89 ± 0.45	98.05 ± 0.08	98.21 ± 0.10	99.93 ± 0.14,	98.26 ± 0.41	<0.001
SPTD	0.233	94.25 ± 0.48	99.54 ± 0.09	100.16 ± 0.10	101.90 ± 0.14	99.72 ±0.43	<0.001

In the group "All dressage horses", the average breeding values (iEBV) steadily increases untill the final IBC group of 0.05<IBC, where they drop slightly. The R^2 remains fairly constant, ranging from 0.208 to 0.243 (a difference of 0.035) indicating a small variance to the distribution of data. The results constantly remain significant with $p<0.001$.

Table 12. Breeding values for dressage horses with own performance in relation to the R^2 for each, over a varietyof IBC classes and the subsequent P-value. TID^{P} = Total Index Dressage with own performance, TCD^{P} = iEBV for tournament competitions dressage with own performance, YCD^{P} = iEBV for Young Horse competitions dressage with own performance, $MPTD^{P}$ = iEBV for dressage with own perfromance in mare performance test and stallion ability test and $SPTD^{P}$ = iEBV for dressage with own performance in stallion performance test. Total population size is N=78 907.

Breeding Value	R^2	IBC=0.00	0<IBC≤0.01	0.01<IBC≤0.02	0.02<IBC≤0.05	0.05<IBC	P-value
TID	0.225	93.58 ± 0.51	98.62 ± 0.09	98.86 ± 0.11	100.65 ± 0.15	98.64 ± 0.46	<0.001
TCD	0.205	95.02 ± 0.43	98.91 ± 0.08	99.22 ± 0.09	100.55 ± 0.13	98.91 ± 0.39	<0.001
YCD	0.239	94.05 ± 0.41	98.11 ± 0.08	97.77 ± 0.09	99.09 ± 0.12	97.63 ± 0.37	<0.001
MPTD	0.228	93.92 ± 0.48,	98.14 ± 0.09	98.26 ± 0.10	100.03 ± 0.14	98.33 ± 0.43	<0.001
SPTD	0.207	94.27 ± 0.51	99.62 ± 0.09	100.22 ± 0.11	102.02 ± 0.15	99.83 ±0.46	<0.001

In the group “All dressage horses with own performance”, once again the average breeding values (iEBV) steadily increase untill the final IBC section of 0.05<IBC where they drop slightly. The R^2 remains fairly constant ranging from 0.205 to 0.239 (a difference of 0.034) indicating a small variance to the distribution of data. The results constantly remain significant with $p<0.001$.

Table 13. Breeding values for all jumping horses in relation to the R^2 for each, over a variety of IBC classes and the subsequent P-value. TIJ = Total Index Jumping, TCJ = iEBV for tournament competitions jumping, YCJ = iEBV for Young Horse competitions jumping, MPTJ = iEBV for jumping in mare performance test and stallion ability test and SPTJ = iEBV for jumping in stallion performance test. Total population size is N=8,724.

Breeding Value	R^2	IBC=0.00	0<IBC≤0.01	0.01<IBC≤0.02	0.02<IBC≤0.05	0.05<IBC	P-value
TIJ	0.066	93.42 ± 0.56	91.70 ± 0.10	90.49 ± 0.12	89.95 ± 0.17	91.23 ± 0.51	<0.001
TCJ	0.134	96.82 ± 0.35	92.63 ± 0.07	90.91 ± 0.08	90.47 ± 0.10	91.21 ± 0.32	<0.001
YCJ	0.139	93.88 ± 0.37	92.75 ± 0.07	91.22 ± 0.08	90.53 ± 0.11	90.73 ± 0.33	<0.001
MPTJ	0.026	94.36 ± 0.57	93.94 ± 0.11	93.77 ± 0.13	93.54 ± 0.17	95.15 ± 0.52	<0.001
SPTJ	0.048	94.06 ± 0.54	92.99 ± 0.10	92.03 ± 0.12	91.57 ± 0.16	92.90 ± 0.49	<0.001

In the group “All Jumping horses”, the average breeding values (iEBV) steadily decrease untill the final IBC section of 0.05<IBC where they rise slightly. The R^2 remains fairly constant ranging from 0.026 to 0.139 (a difference of 0.113) indicating a small variance to the distribution of data, though not as concise as the Dressage subgroups. The results constantly remain significant with p<0.001.

Table 14. Breeding values for jumping horse with own performances (N = 78,907) in relation to the R^2 for each, over a variety of IBC classes and the subsequent P-value. TIJ^P = Total Index Jumping with own performance, TCJ^P = iEBV for tournament competitions jumping with own performance, YCJ^P = iEBV for Young Horse competitions jumping with own performance, $MPTJ^P$ = iEBV for jumping with own performance in mare performance test and stallion ability test and SPTJ = iEBV for jumping in stallion performance test. Total population size is N=78 907.

Breeding Value	R^2	IBC=0.00	0<IBC≤ 0.01	0.01<IBC≤ 0.02	0.02<IBC≤ 0.05	0.05<IBC	P-value
TIJ	0.065	93.72 ± 0.59	91.74 ± 0.11	90.59 ± 0.13	89.98 ± 0.17	91.08 ± 0.53	<0.001
TCJ	0.137	97.17 ± 0.37	92.59 ± 0.07	90.92 ± 0.08	90.43 ± 0.11	91.02 ± 0.33	<0.001
YCJ	0.138	94.13 ± 0.39	92.77 ± 0.07	91.29 ± 0.08	90.56 ± 0.11	90.60 ± 0.35	<0.001
MPTJ	0.025	94.56 ± 0.61	94.02 ± 0.11	93.88 ± 0.13	93.59 ± 0.18	95.06 ± 0.55	<0.001
SPTJ	0.048	94.31 ± 0.58	93.04 ± 0.11	92.13 ± 0.12	91.62 ± 0.17	92.78 ± 0.52	<0.001

In the group "All Jumping horses with own performance", the average breeding values (iEBV) steadily decrease untill the final IBC section of 0.05<IBC where they rise slightly. The R^2 remains fairly constant, ranging from 0.025 to 0.138 (a difference of 0.113) indicating a small variance to the distribution of data, though not as concise as the Dressage subgroups. The results constantly remain significant with $p<0.001$.

The findings of *Table 11* through *Table 14* are summarized in *figure 5* which reflects the total indices for variance with inbreeding coefficient groupings for all horses (dressage and jumping respectively) and all horses with their own performance records (dressage and jumping respectively).

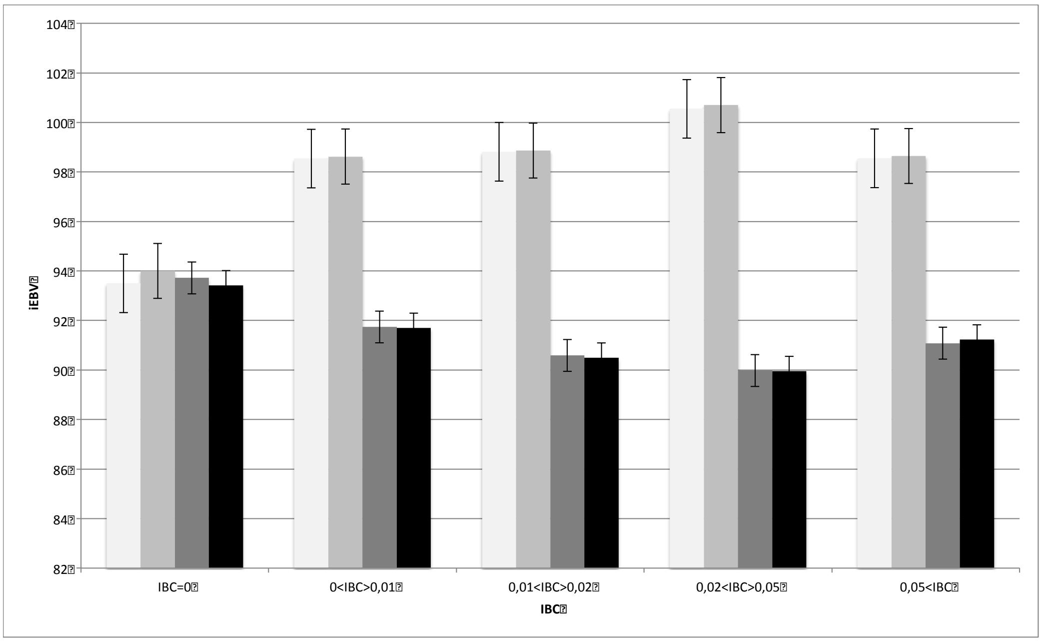


Figure 5. Histogram illustrating the relationship between various IBC classes and iEBV for all dressage horses (□), dressage horses with own performance (□), all jumping horses (■) and jumping horses with own performance (■) for total data groupings (TID and TIJ). All IBC classes have a P-value of less than 0.001.

The data illustrates a significant ($p<0.001$) positive relationship between inbreeding (as measured by IBC) and performance (as measured by iEBV) for dressage and a significant ($P<0.001$) negative relationship between inbreeding (as measured by IBC) and performance (as measured by iEBV) for Jumping (see *figure 5*).

6.2.3 Both Models

In both models, the association of IBC to performance (iEBV) shows a positive relationship in dressage and a negative relationship in jumping.

The dressage results indicate a relatively constant R^2 value from 0.206 (model 1, Total competition data) to 0.243 (model 2, Young Horse competition data) while the R^2 value for the jumping horses was considerably lower than that of the dressage horses and much less consistent, ranging from 0.025 (model 2, mare performance test data for all horses, owb performance, **N =78,907**) to 0.130 (model 2, Young Horse competition data for the entire group of N=84,724 horses) *(Table 15*). This could be indicative of a less focused jumping breeding program as the Hanoverian breeding scheme/program is more focused on dressage.

Though the R^2 value can be described as low, it still indicates a significant relationship between IBC and iEBV with P<0.001.

Table 15. Dressage subgroups in relation to R^2 value for all dressage and jumping horses using Model 1 and Model 2. TID = Total Index Dressage, TCD = iEBV for tournament competitions dressage, YCD = iEBV for Young Horse competitions dressage, MPTD = iEBV for dressage in mare performance test and stallion ability test and SPTD = iEBV for dressage in stallion performance test. Total population sizes are N=84 724 and N=78 907.

	R^2 Model 1 Dressage N =84,724 All horses	R^2 Model 2 Dressage N =84,724 All horses	R^2 Model 1 Dressage N =78,907 All horses own perf	R^2 Model 2 Dressage N =78,907 All horses own perf	R^2 Model 1 Jumping N =84,724 All horses	R^2 Model 2 Jumping N =84,724 All horses	R^2 Model 1 Jumping N =78,907 All horses own perf	R^2 Model 2 Jumping N =78,907 All horses own perf
TID	0.228	0.229	0.224	0.225	0.065	0.066	0.065	0.065
TCD	0.206	0.208	0.204	0.205	0.131	0.134	0.131	0.135
YCD	0.241	0.243	0.237	0.239	0.138	0.139	0.138	0.138
MPTD	0.231	0.233	0.227	0.228	0.026	0.026	0.026	0.025
SPTD	0.210	0.211	0.205	0.207	0.048	0.048	0.048	0.048

All Jumping horses (Total and all subgroups) show a significantly lower R^2 Value compared to that of Dressage horses (Total and all subgroups) in both model 1 and model 2. The results in from model 1 and model 2 are extremely similar, illustrating statistically significant data sets (P<0.001).

Both models and all subgroups have a low error probability (<0.001) indicating significant results with negligible error.

6.3 Comparing the influence of inbreeding to year effect and sex.

Using IBC as a Linear covariate and as a fixed effect, SS figures were used to indicate the relative effect on iEBV (model) of the IBC, sex and year cohort.

Table 16. Independent variables in relation to source (model, IBC, Bsex and year), DF value, Sum of Squares, Mean Square value, F-value and P-value. iEBV Dressage (FE) = Total dressage with IBC as a fixed effect, iEBV Dressage (LC) = Total dressage with IBC as a Linear Covariate, iEBV Jumping (FE) = Total jumping with IBC as a fixed effect, iEBV Jumping (LC) = Total jumping with IBC as a Linear Covariate.

Independent variables	Source§	DF	Sum of Squares	Mean Square	F Value	P value
EBV Dressage (FE)	Model	14	7427981.47	530570.11	1796.71	<0.0001
EBV Dressage (FE)	IBC	4	82838.281	20709.570	70.13	<0.0001
EBV Dressage (FE)	Bsex	1	14440.853	14440.853	48.90	<0.0001
EBV Dressage (FE)	Year	9	7182336.463	798037.385	2702.46	<0.0001
EBV Dressage (LC)	Model	11	7382149.04	671104.46	2268.54	<0.0001
EBV Dressage (LC)	IBC	1	37005.844	37005.844	125.09	<0.0001
EBV Dressage (LC)	Bsex	1	14136.628	14136.628	47.79	<0.0001
EBV Dressage (LC)	Year	9	7358047.651	817560.850	2763.61	<0.0001
EBV Jumping	Model	14	2341692.23	167263.73	424.86	<0.0001

(FE)						
EBV Jumping (FE)	IBC	4	49727.380	12431.845	31.58	<0.0001
EBV Jumping (FE)	Bsex	1	26358.759	26358.759	66.95	<0.0001
EBV Jumping (FE)	Year	9	2205643.922	245071.547	622.49	<0.0001
EBV Jumping (LC)	Model	14	2332843.42	212076.67	538.56	<0.0001
EBV Jumping (LC)	IBC	1	40878.578	40878.578	103.81	<0.0001
EBV Jumping (LC)	Bsex	1	26170.223	26170.223	66.46	<0.0001
EBV Jumping (LC)	Year	9	2240179.853	248908.873	632.10	<0.0001

The relative sum of squares express the variation attributed to the various aspects of; Model, IBC, Sex and Year. Thus the ratio of "SS of the parameter/SS of the model" is used to calculate the variance explained by the different variables in the model.

Dressage IBC FE (IBC as a fixed effect)

The variance explained by inbreeding parameter (IBC) is 82838.281 / 7427981.47 = 1.1%

The variance due to sex 14440.853 / 7427981.47 = 0,19%

The variance due to year effect 7182336.463 / 7427981.47 = 96.7%

Dressage IBC FE (IBC as a linear covariate)

The variance explained by inbreeding parameter (IBC) is 37005.844/ 7382149.04= *0.5 %*

The variance due to sex 14136.628/ 7382149.04= 0.19%

The variance due to year effect 7358047.651 / 7382149.04= *99.7.%*

Jumping IBC FE (IBC as a fixed effect)

The variance explained by inbreeding parameter (IBC) is 49727.380/ 2341692.23 = 2.1%

The variance due to sex 26358,759 / 2341692.23 =1.1%

The variance due to year effect 2205643.922 / 2341692.23 = 94.1%

Jumping IBC LC (IBC as a Linear Covariate)

The variance explained by inbreeding parameter (IBC) is 40878.578/ 2332843.42= 1.8%

The variance due to sex 26170.223/ 2332843.42= 1.1%

The variance due to year effect 2240179.853/ 2332843.42= 96.0%

From this we can see that with a linear covariate or fixed effect through all subgroups, dressage and jumping, the year effect (SS parameter/SS model ± 96%) is by far the dominating factor with IBC (SS parameter/SS model ± 2%) and Sex (SS parameter/SS model ± 1%) fairly insignificant when compared to the model SS.

All subgroups in both dressage and jumping with fixed effect and linear covariate for IBC show a similar result.

6.3.1 Year cohort

The results show a significant positive relationship between the year cohort and the measure of performance (iEBV). *Table 17* and *figure 6* show a progressive increase in the year cohort contribution.

Table 17. Sex (male and female) in relation to Byear, N (subgroup size), IBC (inbreeding coefficient), TID (Total Index Dressage) and TIJ (Total Index Jumping).

Sex	BYear	N	IBC	TID	TIJ	Sex	BYear	N	IBC	TID	TIJ
M	1990	2076	0.0143	82.10	81.90	F	1990	2778	0.0146	81.70	81.28
M	1991	2316	0.0139	83.18	83.45	F	1991	2950	0.0133	83.57	81.95
M	1992	2453	0.0129	85.48	83.18	F	1992	3009	0.0128	85.57	81.85
M	1993	2437	0.0130	87.80	85.11	F	1993	3229	0.0128	87.01	84.39
M	1994	2315	0.0135	89.25	86.29	F	1994	2956	0.0135	89.04	86.13
M	1995	2173	0.0134	91.46	88.04	F	1995	2902	0.0132	91.61	88.07
M	1996	2103	0.0128	93.53	89.42	F	1996	2918	0.0133	94.40	87.70
M	1997	1837	0.0132	95.20	89.69	F	1997	2533	0.0139	95.37	89.36
M	1998	1787	0.0136	95.99	91.57	F	1998	2433	0.0136	96.64	90.63
M	1999	1851	0.0142	98.45	91.09	F	1999	2372	0.0147	99.34	90.06
M	2000	1874	0.0144	100.42	91.19	F	2000	2295	0.0151	101.93	89.50
M	2001	1969	0.0141	101.58	91.32	F	2001	2427	0.0143	103.41	89.28
M	2002	2070	0.0125	103.33	93.37	F	2002	2347	0.0131	105.44	92.21
M	2003	1871	0.0127	104.49	95.79	F	2003	2298	0.0133	106.11	94.35
M	2004	1957	0.0123	106.22	96.42	F	2004	2074	0.0125	107.38	94.86
M	2005	1955	0.0123	106.64	96.52	F	2005	2128	0.0125	108.17	95.13
M	2006	1934	0.0130	107.59	97.18	F	2006	2030	0.0123	109.02	96.63
M	2007	1662	0.0118	109.58	99.85	F	2007	1884	0.0124	111.29	98.46
M	2008	877	0.0120	112.08	101.69	F	2008	1238	0.0126	114.63	99.06
M	2009	3	0.0156	105.67	108.33	F	2009	403	0.0133	119.77	94.20

The performance measure indicates a steady increase from year to year in both dressage and jumping in both male and female cohorts.

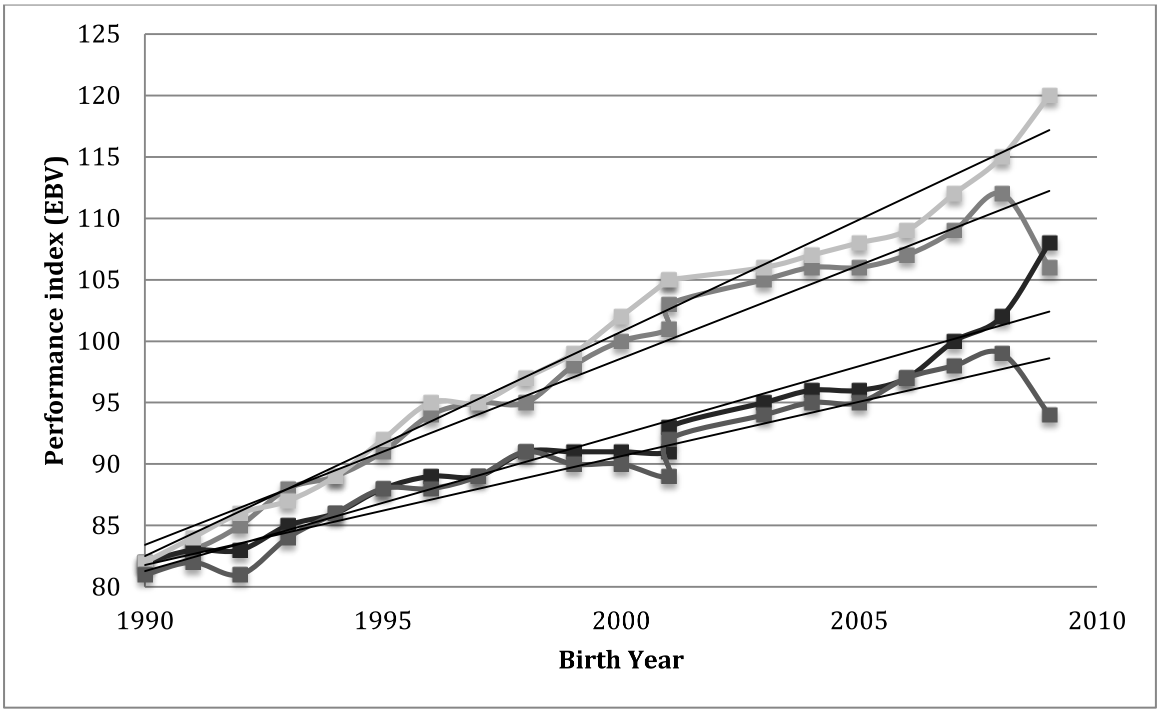


Figure 6. A linear regression illustrating the Performance index (EBV) in relation to the year of birth for TID-Male (▪) with regression equation; y=1.825x-3549.3 and R^2 value of 0.98202, TIJ-Male (▪) with regression equation; y=1.5164x-2934,2 and R^2 value of 0.95599, TID-Female (▪) with regression equation; y=1.1117x-2131.1 and R^2 value of 0.93767 and TIJ-Female (▪) with a regression equation; y=0.8846x-1678.5 and R^2 value of 0.90961. Providing a relative stability of IBC over a number of years for both male and female populations.

The Total Index Dressage (TID) for the male subgroup demonstrates a significant incline over a 20 year period, from a value of 81 units to a final value of 120 units. Likewise, the Total Index Jumping (TIJ) for the male subgroup presents an incline from 81 units to 106 units, hence, there is a significant increase in Performance index for both male subgroups over a period of 20 years. The Total Dressage Index (TID) for the female subgroup, though presented the lowest degree of inclination as opposed to that of the remaining subgroups, still illustrated an incline from 81 units to 94 units. The Total Index Jumping (TIJ) for the female subgroup illustrated a greater incline than that of the Dressage (TID) for the female subgroup, initially presenting a performance index of 81 units and increasing to 108 units over a duration of 20 years.

Chapter 7 Discussion

7.1 The historic use of inbreeding

Inbreeding has shown to be a common principle in the breeding of horses, as practised by advocates such as Tesio (1947). Tesio proposed that his success as a racing breeder (he won twenty-four italian derby races) was largely due to the practise of inbreeding. However, his philosophy on inbreding seems tenuous at best and while many have advicated him a guru, his success has not been repeated with any sort of scientific appraisal of his methods or theories. Even Rasmussen and Faversham (1999) who set out to prove his theories have been criticesd for a skewed data set, with Lyons (2001) arguing that the higher-class runners descend from a narrower range of breeding stock than the population at large. It may be more relevant to view Tesio as simply a great trainer that saw patterns within his breeding and strove to achieve results based on those patterns.

The most relevant paper to this study, is that of Klemetsdal (1998) who found a fourfold reduction in performance in the Norwegian Cold Blooded Trotter with horses inbred to a 15% IBC. Regrettably few other papers have been as decisive with their analysis of inbreeding depression relating to performance.

To this day, inbreeding remains an extremely relevant topic for the modern breeder. Many Warmblood breeders specifically look at the combination of breeding lines and note the number of times certain sires appear in a pedigree. However, within the literature there is a paucity of studies examining the relationship between inbreeding and performance.

7.2 Data

All Warmblood data in Germany is annually collated and performance evaluation computed by the German Vereinigte Informationssysteme Tierhaltung w.V on behalf of the Federation Equestre national (FN), which is the national body for equestrian sport in Germany.

The main advantage of this study is that the Hannoveraner Verband is one of the oldest Warmblood breeding societies and has possibly the most complex and extensive libraries of data; breeding, competition and testing, of any society in the world. Due to the meticulous storing of records and extensive DNA testing of sire, dam and progeny by the Hannoveraner Verband, the breed records demonstrate a high degree of accuracy in terms of pedigree, showing that pedigree records up to the grandparent generation are 100% complete and it is only after the 6th generation that we see a noticeable decrease in pedigree information (less than 80%).

7.3 Data evaluation

The inbreeding was calculated utilising the two methods; Meuwissen method and Van Raden method. This was an effective way of establishing the depth and accuracy of the lineage data set.

The data evaluations relating to the relationship between inbreeding and performance in this study utilises the BLUP-Multitrait-Repeatability-Animal model. The BLUP-Multitrait-Repeatability-Animal model (Meinardus and Bruns, 1987) has been used in Germany for many years and is the most comprehensive analytical system available for analysing the relationship between inbreeding (IBC) and performance (as measured by iEBV). It simultaneously estimates and adjusts for environmental and genetic factors, allowing for the differentiation of a horse due to factors such as its genetic background and/or experience of the rider.

7.4 The Measure of performance

The measure of performance in the horse is wide and varied but generally relates to the goal of the breeder. Breeders of Warmblood horses breed with the goal of performance in sport which is ultimately reflected in actual competition data.

The measure of performance potential calculated by the German Vereinigte Informationssysteme Tierhaltung w.V is the integrated Estimated Breed Value (iEBV). The iEBV performance measure is well known to breeders and serves as the standard in the industry with all breeding values standardised to a relative mean breeding value of 100 with a standard deviation of 20 points (VIT, 2016). All stallion stations in Germany utilise the same system of performance testing when describing their stallions for potential breeding.

While the iEBV remains possibly the best performance measure system currently used for Warmbloods, any system is as good as the data available and evaluating scores from performance tests and Young Horse competitions are still subjective and not comparable over time, across events and type of data sources. As the evaluation of performance tests and indeed dressage events remain a subjective evaluation from judges, there will always remain a variable element of human interpretation. The more evaluations can be standardised, the more accurate the results will become. The more data one has in evaluating the success of a sire, the more accurate the evaluation. Most evaluations now use a combination of Young Horse and adult data which are generally a combination of performance tests and competition results (Luehrs-Behnke and Roehe, 2002) while from a breeders perspective a stallion's worth is often judged from his progeny's success in competition (Hugason and Arnason, 1987).

Further confounding the data set: from a young age the Warmblood horses are tested for potential in either jumping or dressage in a number of ways that include, "Young Horse tests" and "mare and stallion performance testing".

Regretably, most horses are chosen for their predisposition to jumping or dressage based on breeding lines and trained with this specifically in mind in preperation for their performance testing. Data are therefore skewed by breeders predisposition for their training preference based on breeding lines and not necessarily individual potential. Further, often the performance test is seen as the "end product" as opposed to the beginning of a performance career. As such, the distinction and void between breeder and competitor does not allow for the full potential of many horses to be realised and thus data representing a fully accurate portrayal often remains hidden. Many horses who perform averagely for their performance test can be seen later in life outperforming all expectations. A common argument is that breeders breeding for Young Horse tests, produce horses that excel as youngsters with flashy movement that seldom make it to the higher levels of the sport. Thus the "measure of performance" is inheranty flawed, as with the focus on "Young Horse competitions" for many breeders and trainers as an end result, the full potential of horses are often not realised. Therefore performance should be reflected in two distinctly different catagories: Young Horse and higher level. These two distinct datasets reflect two very different breeding and training aims or goals. As such, though the iEBV as a measure of performance is arguably the best currently available, it at best represents an "averaged " performance representation that neither reflects fully Young Horse talent, or older, higher level competition talent.

Further, the iEBV breeding values based on progeny performance may not then be an accurate reflection of the sires worth as the progeny are restricted by the quality of the mares to whom the respective sire is mated. Due to the stringent testing methods of stallions, there are very few, if any, "poor" stallions and as such quality of progeny is generally dependant on mare quality and the interaction of the specific breed lines of sire and mare. Two sires of equal worth may have dramatically different breed values depending on the access of each to quality mares. Though it may be true that quality sires attract quality mares, quality sires also attract average mares with breeders having a inflated view of their breeding stock.

7.5 Inbreeding

The level of inbreeding within the Hanoverian population is low, with a value of around F = 1.5 when compared to other horse populations, such as the Norwegian trotter, at F = 7.5 (Klemetsdal 1998), the Andalusian at F = 8.48 (Valera et al, 2005) and the Friesian at F = 15.7 (Sevinga et al., 2004).

The low inbreeding level for the Hanoverian population is the result of an open studbook, with breeders having access to approved stallions from a variety of studbooks including; the Holstein, KWPN, Oldenburg, Selle Francais, Trakehner, the Anglo Arab and the Thoroughbred. However, with the advent and widespread use of AI (Artificial Insemination) and the resulting use of a smaller pool of select stallions utilised across a wider pool of mares, with sometimes as many as 500 mares bred to a single stallion, this may counter balance the use of an open studbook by creating a smaller effective gene pool. But despite the advent of AI and the resultant diminishing of utilized stallion numbers, the degree of inbreeding has not increased noticably sine the 1990's (Niemann, 2009). This implies that the Hannoveraner breeders, by nature of current breeding practises and trends, tend towards outsourcing as much as the allure of popular top Hanoverian stallions. It is important that breeders remain aware of this by-product of AI and select breeding lines to maintain a diverse gene pool to encourage the genetic diversity an open studbook promises.

Most Warmblood breed societies operate as a "breed type" with and Open stud book. As such, breeders have the lattitide to constantly "outbreed" and utilise new genetic material within the breeding structure. Thus, although the practise of inbreeding to solidify superior characteristics remains prevelant, breeders are also aware of the dangers (even if specific research is scant) and utilise the structure of an open stud book to keep inbreeding at a manageable or "accepted" level. The two aspects of inbreeding practice and an open studbook that encourages a cross pollination of breeding lines, seem to counteract each other and promote a healthy breeding structure without immediate danger of inbreeding depression.

The only performance horse that operates successfully at the same levels of inbreeding as the Thoroughbred seems to be the Friesian at levels up to F = ± 15.7 (Sevinga, et al., 2004). The breed has often been redefined according to current need and trends and has recently focussed worldwide on breeding as a dressage horse. Despite the level of inbreeding, the performance seems to have increased dramatically in recent years, with 2015 seeing for the first time a Friesian competing in the dressage section of the World Equestrian Games. As such, the high level of inbreeding does not seem to have restricted the dressage performance of the breed as yet.

In this study, the IBC for “all horses with Hannoverian sire and dam” were consistantly higher (+-0.4%), year after year, than the group “all horses with own performance”, indicating that even though the IBC is relatively low (+-1.5%), there is significantly higher IBC within the full Hanoverian bred population. This is not an isolated anomally that fluctuates from year to year, but rather a constant pattern that has maintained year for year from 1990 through to 2008. This means that the horses the Hannoveraner breeding program are utilizing to “outcross” and bring in new genetic material are diverse enough from the Hanoverian population to make a significant difference. The system of an open stud book is therefore a positive effect on the diversity of the breed type.

7.6 The measure of inbreeding

The accuracy of the Hannoveraner data set is reflected in the calculationof the inbreeding coefficient, as the calculation relies heavily on the accuracy and depth of the pedigree. This is shown by the two methods (Meuwissen method and Van Raden method) producing identical (100% match) results in this study. If the pedigree data were less extensive, the results would be expected to differ slightly, as Van Raden’s method handles many more generations, distinguishes close from far inbreeding and assumes inbred or related founders (van Raden, 1992).

7.7 Inbreeding – a critical level

Part of the inferred purpose of this study is to establish if there are levels of inbreeding that either enhance or restrict the performance of the Hannoverian as a Sport Horse (Inbreeding depression).

Frankham et al., (1993), argued that selection is able to counteract a significant part of inbreeding depression over time. Likewise, Falconer (1960) and Fikse (1997) both stressed that the problem with the estimation of inbreeding depression was the effect of selection. This was specifically relevant to Warmblood analysis as Warmblood breeding heavily utilises phenotypic selection. This infers responsibility of the breeders to manage levels of inbreeding to keep within acceptable levels that restrict inbreeding depression. This study however does not ascertain any quantifiable level of inbreeding relating to depression in performance. Indeed, there has to date been little evidence recorded that indicates a critical level of inbreeding in the performance of the Warmblood Sporthorse.

7.8 Inbreeding classes

The IBC's were catagorised into 5 classes; IBC=0.00, 0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, and 0.05<IBC.

Within these groupings, there were significant differences of IBC from the first group (IBC = 0) to the remaining groups (IBC >0)(*Figure 5*). The first group (IBC = 0) was lower for dressage horses and higher for jumpers compared to the other groups.There was no immediate indication as to why the performance measure was significantly different for the first group to the remaining four. This may however be an artifact reflective of the Hanoverian population being principally a dressage focussed breed where the majority of the data is derived from dressage-bred horses with jumping essentially a secondary breed trait. Further, in the dressage group, breeders may be focusing on linebreeding with superior stallions within the Hanoverian focussed dressage program with the goal of breeding more competitive horses, whereas the jumper focussed breeders may tend towards utilising approved jumper stallions outsourced from more jumper focused breeding programs.

The largest grouping of horses were in the grouping with nearly zero IBC (0<ibc≤0.01). This grouping had +- 37000 horses in it. The next biggest grouping in terms of numbers was the next grouping (0.01<IBC≤0.02) with marginally higher IBC. This group had +- 27,000 horses. Between these two groupings, where the IBC was 0>IBC≤0.02, this represented = +- 79 % of the horses. Though results are nearly all significant, (p<0.001), inbreeding is indicated at such a relatively low level, to not warrant concern at this stage for any degree of inbreeding depression.

7.9 Inbreeding and performance

7.9.1 The Inbreeding effect in relationship to the standard deviation of iEVB

The dressage horses demonstrated an incline in the iEBV for the higher IBC groups (*Table 11 and Table 12*).

In the dressage group; "all horses N = 84,724" (*Table 11*), the four IBC groups indicating a degree of inbreeding (0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, 0.05<IBC) show limited variation in iEBV (i.e 98.54 – 100.55), which represents 10.05% of the standard deviation of the population. The standard deviation for the population is 20 (VIT, 2016).

In the dressage group; "horses with own performance N = 78,907" (table *12*), the four IBC groups indicating a degree of inbreeding (0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, 0.05<IBC) also indicate limited variation in iEBV (i.e 98.62 – 100.65), which represents 10.15% of the standard deviation in the population.

Further, in the dressage groups (*Tables 11 and 12*), from the least inbred to the most inbred, the deviation of iEBV, LSM groups were from 93.50 (IBC = 0) to 100.65 (0.02<IBC≤0.05), which represents 7.15 / 20 = 35.75% of the standard deviation. Hence a statistically significant regression equation was established for the dressage sub groups and the biological variation from least inbred to the most inbred was approximately one third of the standard deviation in performance.

The jumping horses demonstrated a decline in the iEBV for the higher IBC groups (*Table 13 and Table 14*).

In the jumping group; "all horses N = 84,724" (*Table 13*), the four IBC groups indicating a degree of inbreeding (0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, 0.05<IBC) show limited variation in iEBV (i.e 89.95 – 91.70), which represents 8.75% of the standard deviation of the population.

In the jumping group; "horses with own performance N = 78,907" (*Table 14*), the four IBC groups indicating a degree of inbreeding (0<IBC≤0.01, 0.01<IBC≤0.02, 0.02<IBC≤0.05, 0.05<IBC) also indicate limited variation in iEBV (i.e 89.98 – 91.74), which represents 8.8 % of the standard deviation in the population.

In the jumping groups (*Tables 13 and 14*), from the least inbred to the most inbred, the deviation of iEBV, LSM groups were from 89.95 (0.02<IBC≤0.05) to 93.42 (IBC = 0), which represents 3.47 / 20 = 17.35% of the standard deviation. Hence a statistically significant regression equation was established for the jumping sub groups and the biological variation from least inbred to the most inbred was approximately one tenth of the standard deviation in performance.

Given the trend of IBC in both dressage and jumping horses, there does not appear to be any "real / biological" differences between the IBC classes, given that the standard deviation of the iEBV was 20, and the deviation between most inbred and least inbred varies at the most by approximately 35.75% (dressage sub group) of the standard deviation for iEBV. The lack of biological differences in the IBC groups, may indicate that the findings are spurious results from the large sample size. Further, the fairly tight distribution of most inbred to least inbred, indicates that the effect of inbreeding on the performance, as measured by iEBV was negligable at the current levels of inbreeding. However, the tight grouping of iEBV does remain a positive reflection for the Hannoveraner breeding program as, combined with the effect of the year cohort steadily increasing (*figure 6*), it indicates that the population as a whole is moving in a positive direction in terms of performance.

7.9.2 Jumping and dressage compared

Although few studies have explored the relationship between inbreeding and performance, it was predicted that the correlation for dressage performance and inbreeding level would be the same or similar to that of jumping performance and inbreeding level. This was shown to be incorrect. The results from model 2 of this study indicated that there was a significant ($P<0.001$) positive relationship between inbreeding and dressage performance, and a significant ($P<0.001$) negative relationship between inbreeding and jumping performance (*figure 5*). Model 1 of this study concurs with these results as *Tables 5 and 6* indicate a positive linear regression coefficient for Inbreeding (IBC) for all subgroups of dressage and *Tables 7 and 8* indicate a negative linear regression coefficient for Inbreeding (IBC) for all subgroups of jumping. These results may by indicative of a large percentage of horses being bred for the purpose of dressage in the Hanoverian breed type.

7.9.3 Contribution of IBC to iEBV

Though inbreeding showed a significant ($P<0.001$) positive relationship to dressage and a negative relationship to jumping, it must be seen in perspective: that it accounted for an extremely low contribution to the iEBV values (+- 1% of the breeding value mean of 100 for the iEBV (*Table 9*)) and that inbreeding is also at a relatively low level in the Hanoverian breeding program (±0.015). As such it seems, though a factor breeders should be cognisant of, the level of inbreeding is not a defining principle on which to guide the breeding program.

7.9.4 Year cohort – a significant effect

A linear regression of the Performance index (iEBV) in relation to the year of birth (*Figure 6*) illustrated the significant influence by year effect on the performance index. This was an expected result as the aim of any breeding system is to improve the performance level of a breed in particular disciplines. The average breeding figures collected and calculated per year indicate a positive genetic trend in breeding.

Results indicated that year effect was by far the majority of influence on iEBV, while the IBC and sex effect remained small. For both dressage and jumping (with the IBC as a fixed effect or linear covariate), it was determined that ± 96% of the effect on performance was driven by the year cohort (see *Table 16*) and ± 3% related to sex and IBC.

The performance index directly correlates with that of the year cohort, thus indicating that the breeding program was and currently still is, successful. However, it is unlikeley that that the year cohort is an influencing factor on individual performance, but rather provides an efficient means to categorizing, or sectioning, the various breeding cycles.

7.9.5 contritution of sex to iEBV

Though a significant result ($p<0.001$), the factor of sex had a minor effect of performance, contributing +-1% contribution to the iEBV.

7.9.6 The relative increase in iEBV

The performance index (iEBV) in relation to the birth year of individual horses (*Figure 6*) indicates that over a duration of 20 years, both sexes of dressage and jumping horses have greatly improved in terms of performance. The female subgroup for the Total Index Dressage (TID) illustrated the greatest increase in performance index over 20 years. The male subgroup for Total Index Dressage (TID) indicated the second greatest increase in performance index, followed closely by the male subgroup for the Total Index Jumping (TIJ). The female subgroup for Total Index Jumping (TIJ) presented the lowest increase in performance index of all the subgroups for both dressage and jumping disciplines.

Such results should be viewed conservatively as the use of sires is not sequential according to birth date but rather with the continued use of older sires. As such performance data uses mixed birth years of sires and it would be unlikely that the models systematically over-estimate the younger birth years. Focus should therefore be minimal on the increase in specific iEBV values, but rather on the comparative effect of year to the other traits observed.

Further in context, it must be noted that as the equine BLUP data does not measure "real production" such as milk solids or litres of milk, the data may reflect an artificial increase in iEBV as an artifact of the subjective testing of CPT's, Young Horse competitions and dressage competition judging.

7.9.7 A constant IBC

This study indicates a relatively constant inbreeding coefficient of approximately of ± 1.5 % from 1990 through to 2013. With the studbook remaining open, and given the large size of the Hanoverian studbook (± 6000 foals per year), it seems unlikely that the inbreeding coefficient could reach a level to achieve a biologically quantifiable effect on performance. However, an increase in inbreeding in relation to that of performance, does not necessarily follow a linear relationship. Klemetsdal (1998) in a population of Norwegian trotters showed a curvilinear effect of inbreeding with performance and found that a doubling of the inbreeding coefficient will quadruple depression. Therefore it would be wise, even though the current level of inbreeding in the Hanoverian horse is thought to be low, be hesitant to allow it to increase.

Further to this, a "criticial level " for the Hannoveriann horse performance has not yet been established. The concept and understanding of a critical level of inbreeding is indeed poorly understood and seems to vary from breed to breed as horses like the Friesian, with an IBC of around 15%, still seems to be excelling in the performance sport of dressage.

Chapter 8 Limitations

Generally in studies of this nature, the most limiting factor is the quality and depth of pedigree avaliable in the data set. In this study, pedigree information was 100% accurate up until the grandparent generation and only after the 6th generation did the pedigree accuracy drop to below 80%. This indicates a very high degree of accuracy in the results pertaining to the calculation of the IBC. This was endorsed by identical results (100% fit) from the use two different methods (Meusen and the van Raden methods) for calculating the IBC of the data. .

However, a major limitation in this study was the low level of IBC in the Hanoverian population (F = +- 1.5%). A population with a higher average IBC may yield different results.

As the results of any study are as accurate as the quality of the data inputed, the principle concern of this study would be the subjective nature of initial data relating to the performance index (iEBV). This is especially relevant for data pertaining to evaluating performance test scores, Young Horse competitions and dressage competitions, as these are not comparable over time, events or data sources. The more standardised these can become, the more accurate the iEBV measure will be. This is a constant concern for most breed societies and it is an area where improvement is often sought. To this end the Hannoveraner Verband endeavours to limit the total number of judges used (and thus number of differing subjective views), while insisting on a minimum number of judges specifically for stallion tests. This methodology could be improved as the minimum number of judges required for mare performance tests (one) is less than for stallion performance tests (two). Further to this, the stallion testing is generally far more intensive than the mare testing, and over a longer period of time (generally a single day test for mares, but a 70 day test for stallions). While this may be justified by the importance placed on the stallions in that a single stallion can produce hundreds of offspring, it does not help the true representation of the breed within the data set when the mares are dramatically less tested than the stallions and the geldings are not tested at all (other than in adult horse competition). For optimum results in a study such as this, though economically not viable, mares and geldings would need to receive the same intensity of testing as do stallions.

The disparate subjective influence when comparing the judging of jumping horses and dressage horses allows for concern for the comparative results between the two groups. In competition, dressage judging is subjective (dressage scores are subjective “marks” from judges), while jumping is non-subjective (a non-subjective “pole down” is awarded marks against the horse/rider combination). As such, the distribution in performance results of jumping focussed horses to dressage focussed horses could be influenced by sets of more and less subjective scores assigned, thus altering the relationship of iEBV to IBC. This comparative effect is amplified in Young Horse competitions and performance testing as the comparative subjective interpretation between judging a dressage horse and judging a jumping horse may allow for greater disparity as it could be argued that a greater difference can be seen between a good jumper and a bad jumper and a good dressage horse and a bad dressage horse. This would influence comparative performance test results.

Further limiting the scope of performance data is the fact that many of the best horses do not always make it into competition. This may be attributed to factors such as;

- Injuries early in a career.
- The best riders are not always available for the best horses.
- Trainers are not always available for the best horses.
- Good horses may be exported and as such their performance data is not available for study.

This will constitute a large proportion of competition talent that is never realised and as such limit the scope of the study. Further to this point, many mares and stallions complete their mare and performance tests and move straight into breeding (Dubois and Ricard, 2007). Many of the best stallions are, for economic reasons, "retired" to breeding and therefore do not reach their potential. If they were entered into the competition arena, the competition aspect of the iEBV would adjust accordingly. Though Huizinga et al., (1991) found high heritability for movement traits to later sport competition, the heritability of movement traits does not necessarily translate into competition success.

The large environmental effects of phenotype indicate the need for collection of data over a long time frame to get accurate resuls. But even then the bias of preselection of specific breeding lines for different disciplines would indicate a possible over-inflation of true heritability and affect results. The pre-selection process begins with the breeder who initially decides whether a horse goes into competition, bred with, is gelded, or left entire. These decisions are based on a variety of factors; breed, performance and personal, such as; opinion on breed lineage, current trends, marketability, stocking levels, the ability of the stud to handle stallions, and various other economic factors. Preselected for a sport direction (dressage or jumping) based on lineage, eliminates a large proportion of potential data where jumping horses could (and have often been shown to) show great potential in dressage, while dressage bred horses could contribute significantly (either positive or negative) by adding to jumping data.

Though the Hanoverian breed has established a "jumping book", the Hanoverian still remains a heavily focused dressage breed. As such, much of the jumping data is derived from dressage bred horses (especially in performance testing) where the jumping aspect of their iEBV is very much a secondary breed trait. The structure of the breed testing ensures that jumping stallions still have three good basic paces (the "dressage" portion of the testing), while less importance is placed on dressage stallion's ability to jump. This also translates to the philosophy of the breeders. Breeders will endeavor to breed good movement into a jumping stallion while very few breeders will endeavor to breed a good jump into a dressage stallion. This natural tendency to breed "dual ability" jumpers while allowing "single ability" dressage stallions, will tend to skew the data from jumping to dressage traits.

There are always many factors influencing genetic expression, especially when it comes to performance. In a non-lab environment such as the extremely diverse world of commercial and non-commercial horse breeding, many non-genetic factors may influence research and results, rendering a hypothesis null and void. For example, racing times for the Thoroughbred horse have been relatively static since 1910 (Hill, 1998). Various researchers have indicated that this may be due to inbreeding depression as the Thoroughbred remains one of the most inbred breeds of the world (Cunningham et al. 2001). However, with horses such as the Friesian having a comparative IBC of +-15%, and still seemingly improving dressage performance internationally, it indicates that possibly the restriction on Thoroughbred performance may not be genetic but rather physical: that the horse simply cannot go any faster anatomically.

Chapter 9 Future Research

Advantageous for the focus of future research is to utilise a population where inbreeding depression is most obviously a limiting factor to evaluate the relevant critical level of IBC as pertaining to performance. Further needed is to establish the varying aspects of performance and how they individually and cohesively relate to such inbreeding depression. It is pertinent to establish how the different performance criteria are influenced at varying levels of inbreeding.

As it seem that different breeds react differently to varying levels of IBC and performance, a single study on one particular breed or breed type should not be viewed as definitive.

The current study of the Hanoverian horse, revealed a low level in inbreeding (F = +-1.5). This study indicates that this level may not be high enough to indicate any real effect on performance. Thus utilising a population with a higher average inbreeding coefficient would be beneficial for future research. Further, as the Hanoverian breeding program is dressage heavy, a study using a jumping focused breed book would also be advantageous as a further comparative. Both of these indications (a higher average IBC and a jumper focussed breeding program) may be found in the Holsteiner breed. Further in this vein, the comparison of a jumper heavy population and a dressage heavy population with an equivalent IBC level could yield interesting results, and if data allows, it would be good to split the competition aspect and the breed performance aspect of the equations.

As the Thoroughbred is one of the most highly inbred horses (F = +- 15%), it seems that it is also an obviously candidate for future research. However, since the racing times have not improved since 1910, it seems that the horse may have reached it's peak anotomical speed. Before further research on the genetic limitation of sped in the Thoroughbred, it seems that research into the mechanical observation of limitations would be pertinent. However racing is not the only measure of performance applicable to the Thoroughbred horse. They are extensively used in dressage, jumping and eventing. As such, performance levels in these sports should be explored to establish if they too have plateaued. Initial thought is they have not, which would indicate that the Thoroughbred's performance is not restricted through inbreeding depression and would thus substantiate the hypothesis that the Thoroughbred's racing performamce limitation is anatomical.

At a comparative inbreeding level to that of the Thoroughbred is the Friesian horse (at F = +-15%). This horse does not seem to have been restricted in dressage performance by such a high level of inbreeding. Indeed the Fresian horse seems to be improving it's dressage performance in recent years with 2015 seeing the first time the Fresian horse breed has been represented in dressage at the World Equestrian Games. As such, it seems that a similar study of the correlation between inbreeding and performance in the Fresian horse would provide interesting results.

A restricting factor to our study is the diversity of performance data (Young Horse competitions, performance tests, actual competitions), providing a dataset with extremely diverse performance measures. Breeders often focus on Young Horse competition breeding, though results indicate that often horses that excell at Young Horse competitions do not necessarily excell at the higher levels of competition at older age goups. As such the disparate focus on Young Horse competitions and higher level competition, creates a skewed sense of true competition value and generates an inherent bias within the data. This strengthens the argument to utilise two different performance measures for performance and thus two different models for the relationship between inbreeding and performances. It would be especially relevant to segregate Young Horse competition results and advanced competition results to establish if there is a differing degree of inbreeding influence on these datasets. The Performance Test data provides yet another measure of performance within the performance measure of iEBV. It would therefore be highly advantageous to also separate this as a separate measure of performance.

The data set of this study has not only these three performance measures grouped together, but also includes a large amount of "white noise" that distracts from relevant data. This relates to horses that have no quantifiable competition data such as geldings not competed. A group with nearly as little data available are mares that are tested once in their lives (in a one day performance test) and "retired" to stud. Future research would benefit from eradicating this "white noise" from the dataset.

The most relevant test in performance is horses that have competed over several years and reached a higher level. Specific research of inbreeding pertaining just to this group of horses would be most beneficial.

Chapter 10 Conclusion

The hypothesis: "that inbreeding in the Hanoverian Sport Horse is associated with better performance," can be rejected. Results have significantly illustrated a positive effect of inbreeding on dressage performance as opposed to that of jumping performance. However, inbreeding was deduced as negligible for overall individual performance with regards to the inbreeding effect.

The different sexes indicated a lack of difference in overall performance, and as such, should not be included as a limiting factor to the evaluation of individual performance.

Year cohorts illustrate the importance of categorising breeding cycles within various breeding programs. The increase in years showed a positive correlation with that of average performance in the equine population. This demonstrates the success of the current Hanoverian breeding program.

There is little or no concern to adjust the breeding structure in the breed as the inbreeding level has remained relatively constant for the past 20 years at approximately 1.5% At this level, there is little or no effect on performance (though statistically significant) compared to other factors such as year effect.

Chapter 11 References

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Chapter 12 Appendices and Annova – see CD attached