



Population genetic analysis and breed assignment of three Swedish horse breeds

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CONTENTS

<u>Abstract</u>	1
<u>Svensk sammanfattning</u>	1
<u>Introduction</u>	3
Background	3
Brief history of the Swedish Standardbred	3
Origin of the North Swedish Horse	4
Brief history of the North Swedish Trotter	5
World records	6
Genetic testing and breed assignment	6
Previous results	7
Aims of study	7
<u>Materials and Methods</u>	8
Sampling of populations	8
Data set	8
Statistical analysis	8
<u>Results</u>	9
Heterozygosity	9
Deficiency in heterozygosity	9
F-statistics	10
Nei's distance	10
Breed assignment	10
<u>Discussion</u>	11
Genetic population analysis	11
F _{st} comparison	12
Cluster assignment	12
Is high BLUP correlated to previous crossbreeding between the North Swedish Trotter and the Standardbred?	12
Conclusion	12
Acknowledgments	13
<u>References</u>	14
Appendix 1	18
Appendix 2	22
Appendix 3	23

ABSTRACT

The genetic relationship between three Swedish horse breeds was investigated using microsatellite data from 144 loci in 30 horses. The North Swedish Trotter is believed to have been crossed with the Standardbred in the 1950's to produce a faster trotter. If true, the North Swedish Trotter should be more alike the Standardbred than what the North Swedish Draught Horse is, from which they originate. This was investigated using F-statistics and Nei's distance in GENEPOP and GENETIX and cluster assignment in STRUCTURE. All three breeds were assigned to clearly separate clusters but the genetic relationship between the North Swedish Trotter and the Standardbred was closer than the relationship between the Standardbred and the North Swedish Draught Horse.

SVENSK SAMMANFATTNING

Det genetiska förhållandet mellan tre svenska hästraser undersöktes med hjälp av mikrosatellitdata från 144 loci hos 30 individer. Under 1950-talet ansågs den nordsvenska travaren ha korsats med varmblodstravaren för att få fram en snabbare kallblodstravare. Detta borde kunna ses genetiskt genom att den nordsvenska travaren då skulle vara mer lik varmblodstravaren än vad den nordsvenska brukshästen är, från vilken den nordsvenska travaren härstammar. Detta undersöktes genom beräkningar av F-statistik och Nei's genetiska avstånd i GENEPOP och GENETIX och rastillhörighet i STRUCTURE. Alla tre raserna tillhörde separata grupper men det genetiska förhållandet mellan den nordsvenska travaren och varmblodstravaren var närmare än det mellan varmblodstravaren och den nordsvenska brukshästen.

INTRODUCTION

Background

This study deals with genetic comparisons of two Swedish trotting breeds and the North Swedish Draught Horse. In Sweden horseracing is a very popular sport. Equine trotting alone used about 11 billion Swedish kronor in 2007 (www.atg.se). The two most common breeds of trotters in Sweden are the North Swedish Trotter and the Standardbred and the populations are estimated to 7 000 and 58 000 respectively. This makes the Standardbred the second most common horse breed in Sweden after the Swedish Warmblood. There are also about 7 000 North Swedish Horses in Sweden (<http://www2.sjv.se>).

Brief history of the Swedish Standardbred

The Swedish Standardbred (Figure 1), being lighter and faster than the North Swedish Trotter, stems from crosses between the American and the French Trotters. The breeding of the Swedish Standardbred began in Sweden sometime in the early 1900's. The Swedish Standardbred has had its own studbook since 1950 (www.fao.org/dad-is/). In the United States in the late 1700's a famous Thoroughbred stallion called Messenger produced offspring that were very good trotters. These offspring were crossed with the now extinct Norfolk trotter, through a stallion called Bellfounder, and the trotting abilities of the offspring were further improved (Falk-Rønne, 1988). In 1849 a grandson of Messenger, as well as of Bellfounder, was born and was named Hambletonian. This stallion became the common ancestor of all American trotters of today and can also be found in pedigrees of almost all Swedish Standardbreds (www.travsport.se). The French trotters also originate from Thoroughbreds. In the beginning of the 18th century the Arabian stallion Godolphon Arabian produced offspring that showed good trotting abilities. The French trotters were used in the army and were therefore heavier and more robust than the American trotters. In 1937 a 4-year-old American Standardbred stallion called Bulwark was imported and premiered at Solvalla and became the most important Standardbred stallion in Swedish trotting. His most famous offspring was a mare called Frances Bulwark (Falk-Rønne, 1988).



Figure 1. Standardbred at Vincennes, France, copyright © David Monniaux.

Origin of the North Swedish Horse

The assumed ancestor of The North Swedish Horse (Figure 2) as well as other coldblooded horses in Northern Europe is a prehistoric horse shown to have existed in Northern Europe sometime during the Pleistocene period, i.e. about one million years ago. This large and heavy horse evolved into the diluvian horse, *Equus caballus silvaticus*, that lived and thrived in the cold and humid climate of Northern Europe. The horse survived the ice-age and was then called the Forest Horse, *Equus caballus germanicus*, but probably went extinct about 2000 years ago. The closest living relative to the Forest Horse today is the French coldblooded horse, the Poitevin (<http://sv.wikipedia.org/wiki/Skogsh%C3%A4st>). The North Swedish Horse was also heavily influenced by the Norwegian Døle horse, as trading of horses between Norway and Sweden was common in the late 1800's. In the year of 1900 it was first defined as a breed of its own and 1915 the first national studbook for the North Swedish Horse was printed (Dyrendahl, 1999).



Figure 2. North Swedish Horse, copyright © Henry von Platen.

Breed history of the North Swedish Trotter

The North Swedish Trotter originates from the North Swedish Horse (Dyrendahl, 1999). In the early 1900's the North Swedish Horse began to separate into two breed subtypes, a heavier draught horse used in farming and forestry, and a lighter horse used for racing. In the beginning of the 1940's several North Swedish Trotters resembled the lighter Standardbred and it was believed that in order to get a faster trotter, North Swedish mares were crossed with Standardbred stallions. About 30 North Swedish Trotters were disqualified from racing between 1943 and 1959 because they resembled the Standardbred too much (Dyrendahl, 1999). Some of these can be seen in Table 1 (www.travnet.se; www.travsport.se). In 1964 the North Swedish Horse was officially separated into two breeds, the North Swedish Draught Horse and the North Swedish Trotter (<http://sv.wikipedia.org/wiki/Nordsvensk>) and in 1965 the two breeds were separated with two separate studbooks (Dyrendahl, 1999). In 1969 bloodtyping of coldblooded trotters was introduced in order to reduce any possible cheating (www.travsport.se). The most important stallion for breeding purposes in the North Swedish Trotter is a horse called Steggbest (Falk-Rønne, 1988) and in the studbook of North Swedish Trotters of 2008 there were 128 recognised stallions (<http://www.sleipner.org/>). Over the last half century, the trotting speed of the North Swedish Trotter has greatly improved.

Table 1. List of some North Swedish Trotters that were excluded from racing for resembling the Standardbred too much

Horse	Born	Parents
Lisette	1935	Ceres E. Ulrik Draga II
Solatla	1957	Solo Sigrid-Attila
Göken	1955	Solo Skrymer Docka
Paven	1964	Pavin Torrvinbläsa
Toftejänta	1957	Tofteruggen Primsy
Miranda	1959	Mindin Solsippan
Seiviva	1958	Torvinn Seiva
Solros	Missing data	Missing data
Cerafin	Missing data	Missing data
Brommajäntan	Missing data	Missing data
Rusine	1941	Rusar Perla
Solong	1941	Solo Blända
Jacobin	1942	Solo Docka II
Soloboy	1943	Solo Björsila

World records

In 1938 the world record for Standardbreds, 1.11.6 min/km, was achieved by the horse Greyhound (Jacobsson, 2007). Around that same time, in 1934, Centaur became the first North Swedish Trotter to run 1.40.0 min/km. In 2005, Järvsöfaks (Figure 3) became the fastest Coldblooded horse ever when he ran 1.17.9 min/km. The corresponding record for Standardbreds is 1.08.9 min/km, run by Victory Tilly in 2002 (www.travsport.se). These world records have thus improved by about 23 seconds over 71 years for the Coldblooded breeds and by about 3 seconds over 64 years for the Standardbred. One possible reason for this might be the improved racing tracks for the two breeds where the North Swedish Trotter probably experienced the biggest change, going from iced over lakes to today's tracks.



Figure 3. Järvsöfaks at Gävle 2008, copyright © Jonny Birgerg.

Genetic testing and breed assignment

In order to resolve any questions regarding breed assignment, genetic testing can be of help. Cañon *et al.* (2000) used microsatellite data in their investigation of genetic divergence between different breeds of Spanish horses. These breeds of horses have for a long time existed in reproductive isolation due to geographical location, thus reducing gene flow between breeds, and the populations are fairly small. Thirteen loci in individual horses from seven Spanish Celtic breeds and the Thoroughbred were analysed. F_{st} values between pairs of breeds ranged from 2.6% to 15.0%. The study also showed that microsatellites can be used to correctly assign horses to specific breeds with high accuracy.

Microsatellite data have also been used to assign other species to clusters. MacHugh *et al.* (1998) investigated the genetic structure of seven European cattle breeds using microsatellites. Twenty loci from seven breeds were genotyped and F_{st} values were calculated and breed assignment investigated. All seven breeds grouped well into seven separate cluster with only one breed having individuals assigning to several clusters.

The genetic relationship between several breeds of horses have been investigated. Bjørnstad and Røed (2001) used genotype information from 26 microsatellite loci in four indigenous Norwegian breeds and four other breeds of horses and investigated the genetic demarcation of the breeds as well as breed allocation of individual horses. The study showed a high level of correct assignment for all breeds. Only 10% of individuals associated with the "wrong" breed. Using 20 loci, the different breeds were assigned to the correct group 96% of the time. The Icelandic horse separated into two clusters, one between the Shetland Pony and the Nordland/Lyngen horse, the other between the Fjord horse and the Coldblooded Trotter, thus suggesting a mixed ancestry of the Icelandic horse. The study also showed the close genetic relationship between the Døle Horse and the Norwegian Coldblooded Trotter where 7.5% of Døle horses were associated with the Coldblooded Trotter. The Coldblooded Trotter was developed from light Døle horses. Bjørnstad *et al.* (2000) examined the genetic structure of the same four Norwegian breeds as in their later study (2001) and using F-statistics found that the Døle Horse and the Norwegian Coldblooded Trotter differentiate by about 8%. The Norwegian Coldblooded Trotter and the Standardbred show a differentiation of about 21% for comparison. The studbooks for the Coldblooded Trotter and the Døle horse are still open.

Thirstrup *et al.* (2008) used microsatellite data from three indigenous Danish breeds of horses in their investigation on genetic relationships. Microsatellite data was used to investigate the genetic variation of the three breeds and also to see to what degree individuals could be assigned to clusters, using the genetic software STRUCTURE 2.2. F_{st} values ranged from 0.0577 to 0.1406. Two of the breeds investigated were correctly assigned to the right cluster. The third breed was assigned to two separate clusters.

Previous results

As previously mentioned the trotting speed of the North Swedish Trotter has greatly improved over the last half century. Jacobsson (2007) used microsatellite data from the North Swedish Draught and Trotter Horses and the Standardbred to search for genes that regulate physical performance in the horse. 167 loci in the three different breeds were analyzed and F-statistics were used in order to quantify the genetic variation within and between the breeds in an attempt to find chromosome regions under selection. The study showed that the F_{st} values between the North Swedish Trotter and the Standardbred, 0.138, was slightly lower than the F_{st} values between the North Swedish Draught Horse and the Standardbred, 0.144, thus supporting the possible genetic crosses between the North Swedish Trotter and the Standardbred.

Aims of study

The objective of the present study was to further investigate the genetic relationship between the North Swedish Draught Horse, the North Swedish Trotter and the Standardbred and to analyze the data produced by Jacobsson (2007) using different methods of analysis.

MATERIALS AND METHODS

Sampling of populations

The North Swedish Trotter stallions used in the study were selected based on high performance as determined by Best Linear Unbiased Prediction, or BLUP. Care was also taken not to choose horses that were closely related; all but one had different grandparents. The ten Standardbred stallions as well as the ten North Swedish Draught Horse stallions were chosen at random from the genetic database at Sveriges Lantbruksuniversitet, SLU, in Uppsala, Sweden. Basic information on the three horse breeds is shown in Table 2.

Table 2. Basic information on the three horse breeds used in this study. Number of individuals in the populations are based on numbers from 2003

Population	No. individuals sampled	No. individuals in population	Start of studbook
North Swedish Draught Horse	10	7 000	1915/1965
Swedish Standardbred	10	58 000	1960
North Swedish Trotter	10	7 000	1965

Data set

In Jacobsson (2007) a total of 167 microsatellite markers were genotyped but all individuals did not have data for all loci. In this study, 28 of the loci were genotyped again to complement the already existing data. The same genotyping methods were used as by Jacobsson, 2007. Loci where data was missing for more than 50% of individuals of any one breed were excluded, as well as the locus LEX003 because it is located on the X-chromosome, thus leaving a new total of 144 loci. See Appendix 1 for further details on loci used in the study.

Statistical analysis

GENEPOP on the Web version 3.4 (Raymond *et al.*, 1995) was used for initial statistical analysis. Hardy-Weinberg Equilibrium (HWE) was tested for each locus by estimation of exact p-values using the Markov chain method and for the populations using the Fisher's method. Pairwise F_{st} between the three breeds were computed as in Weir and Cockerham (1984) and allele frequencies for each locus were calculated. F_{st} , or fixation index, is used to quantify genetic variation between populations and describes any reduction in heterozygosity compared to what can be expected from a population that is in Hardy-Weinberg equilibrium.

GENETIX 4.05 (Belkhir *et al.*, 1996-2004) was used to calculate F_{is} as in Weir and Cockerham (1984) in order to investigate heterozygote deficiency, or inbreeding.

GENETIX was also used to calculate Nei's distance (1972) as well as expected and observed heterozygosities.

STRUCTURE 2.2 (Pritchard *et al.*, 2000) was used to investigate the number of clusters in the microsatellite data and to assign individual horses to a population, or breed. See Appendix 2 for instructions on how to run STRUCTURE 2.2. STRUCTURE 2.2 computes the likelihood that a given genotype originated in a specific population and it can thus be investigated to what population the North Swedish Trotter belongs. The program uses a Bayesian Markov chain Monte Carlo (MCMC) approach. By using genotype data from multiple loci, it also identifies the number of clusters (breeds or populations) in the sample and simultaneously assigns individuals to these clusters. K (assumed number of populations) was set to 3 and STRUCTURE 2.2 was run with the "admixture model", 10 000 burn-in steps and 100 000 MCMC replicates.

RESULTS

Heterozygosity

A population is described as being in Hardy-Weinberg equilibrium when mating, and thus union of gametes, is random. None of the three populations were in Hardy-Weinberg equilibrium, thus indicating that the breeds are under the influence of genetic selection. The number of alleles at each locus varied between one (for example ASB9) and 16 (COR070) with the average being 7.17 for all three breeds. Number of alleles for all 144 loci are listed in Appendix 3. As shown in Table 3 the average number of alleles per locus was highest for the North Swedish Draught horse, 4.75, which also showed the highest expected heterozygosity, H_e , 0.666. The Standardbred showed the lowest H_e , 0.627, and also the lowest average number of alleles per locus, 4.40. The North Swedish Trotter had an H_e of 0.649 and 4.53 as average number of alleles per locus. Following this the North Swedish Draught Horse also showed the highest observed heterozygosity, H_o , 0.709. Contrary to H_e , however, the Standardbred showed the second highest H_o , 0.699, and the North Swedish Trotter showed the lowest H_o , 0.692. See also Appendix 3 for a list of all loci and their H_e and H_o .

Deficiency of heterozygosity

None of the three breeds showed any deficiency in heterozygosity, or inbreeding, as shown by F_{is} values in Table 3, F_{is} . The highest value was shown in the North Swedish Trotter, 0.00509, and the lowest value in the Standardbred, -0.05277. This difference could be due to the difference in population size seen between the breeds. The F_{is} of the North Swedish Draught Horse, -0.00328 was in between the two other breeds.

Table 3. Results of overall estimates of genetic analysis, N shows the number of individuals, H_e and H_o show expected- and observed heterozygosity respectively, F_{st} represent pairwise comparisons with the North Swedish Trotter, F_{is} shows the deficiency of heterozygosity within a breed

Population	N	H_e	H_o	Average no. Alleles	F_{st}	F_{is}
North Swedish Draught	10	0.666	0.709	4.75	0.084	-0.00328
Standardbred	10	0.627	0.699	4.40	0.141	-0.05277
North Swedish Trotter	10	0.649	0.692	4.53	-	0.00509

F-statistics

F_{st} is a way to quantify the genetic variation between populations. Estimated pairwise F_{st} values across all loci are shown in Table 4. As expected, the lowest F_{st} , 0.084, was detected between the North Swedish Draught and Trotter horses. F_{st} between the North Swedish Trotter and the Standardbred, 0.141, was almost the same as that between the North Swedish Draught and the Standardbred, 0.143.

Table 4. Overall F_{st} -values between the three breeds

Population	North Swedish Draught Horse	Standardbred
Standardbred	0.143	-
North Swedish Trotter	0.084	0.141

Nei's distance

The results of the calculation of Nei's distance are shown in Table 5. As expected, the North Swedish Draught Horse and the North Swedish Trotter showed the shortest genetic distance, 0.367. The two breeds most far apart from each other were the North Swedish Draught Horse and the Standardbred, 0.524. The genetic distance between the North Swedish Trotter and the Standardbred was 0.503. The two breeds were not as closely related as the North Swedish Draught Horse and the Trotter, but at the same time not as far apart as the Draught Horse and the Standardbred. If there had been no crossings between the Standardbred and the North Swedish Trotter in the 1950's, one would have expected the two breeds to be as far apart as the Standardbred and the North Swedish Draught Horse.

Table 5. Nei's distance (1972) between the three breeds

Population	North Swedish Draught Horse	Standardbred
Standardbred	0.524	-
North Swedish Trotter	0.367	0.503

Breed assignment

Results showed that all three breeds were correctly assigned to three separate clusters (Table 6). A slightly higher proportion of the North Swedish Trotter alleles (0.992)

than the North Swedish Draught Horse (0.974), or the Standardbred (0.982), had a membership to an inferred cluster. The North Swedish Draught Horse showed a 2.4% membership of alleles to the same cluster as the North Swedish Trotter and a 0.2% membership to the cluster of the Standardbred, giving the ratio 12:1 (North Swedish Trotter:Standardbred). Calculating the same ratio for the Standardbred showed a 2.6:1 ratio between the North Swedish Trotter and the North Swedish Draught Horse. Finally, the ratio between the North Swedish Draught Horse and the Standardbred shown by the North Swedish Trotter was only 2:1. The ratios thus showed that the North Swedish Trotter only had twice the number of alleles assigned to the North Swedish Draught cluster compared to the cluster of the Standardbred.

All individuals but two of the North Swedish Draught horses were assigned to the proper cluster at the 0.99 level. The corresponding number for the Standardbred was three, and for the North Swedish Trotters two individuals were not assigned to the proper cluster at the 0.99 level. None of these individuals were mis-assigned.

Table 6. The estimated proportion of membership of the three given populations into the three inferred clusters

Given population	Inferred clusters			Number of individuals
	1	2	3	
North Swedish Draught	0.002	0.974	0.024	10
Standardbred	0.982	0.005	0.013	10
North Swedish Trotter	0.003	0.006	0.992	10

DISCUSSION

General population analysis

The breed with the highest average number of alleles per locus, the North Swedish Draught Horse, also showed the highest expected and observed heterozygosity. The North Swedish Trotter, however, showed the lowest observed heterozygosity despite the second lowest expected heterozygosity. This may be a sign of genetic selection in the North Swedish Trotter. Something that relates to this is the calculations of F_{is} . None of the three breeds investigated here showed any deficiency in heterozygosity as measured by F_{is} . However, the North Swedish Trotter showed the highest F_{is} value, something that could signify that the effective population size for this breed is smaller than for the other two and that genetic selection has occurred. The calculations of Nei's distance showed that the North Swedish Trotter was closest to the North Swedish Draught Horse. Interestingly, however, the North Swedish Trotter was closer to the Standardbred than the North Swedish Draught Horse was. This might be as a result of crossing Standardbred stallions with mares of the North Swedish Trotter.

F_{st} comparison

F_{st} values between the North Swedish Trotter and the North Swedish Draught Horse calculated here were similar to those between the Døle Horse and the Norwegian Coldblooded Trotter (Bjørnstad et al., 2001). The Døle Horse was used in the late 1800's in Sweden to create the North Swedish Draught Horse. The Norwegian Coldblooded Trotter, however, showed a lower differentiation to the Standardbred (Bjørnstad et al., 2001) than the corresponding value between the North Swedish Trotter and the Standardbred calculated here. Bloodtyping was introduced later in Norway than in Sweden and Norwegian trotters are generally a little bit faster than Swedish trotters. This opens up for the possibility that there has been somewhat more introgression of the Standardbred into the Norwegian Coldblooded Trotter (Kaj Sandberg, personal communication).

Cluster assignment

All three breeds were well assigned to a cluster of their own, with no individuals assigned to the wrong cluster. If the North Swedish Trotter had no genetic connection to the Standardbred one would have expected the ratio of assigned alleles to be closer to that of the North Swedish Draught Horse, 12:1. Thirstrup (2008) did the same cluster analysis with three Danish horse breeds but found the Danish breeds were not as well assigned as the three Swedish breeds investigated here with one breed, the Knaubstrupper, assigned to two clusters. The Danish breeds, however, had more alleles per locus than the Swedish breeds and the Knaubstrupper still has an open studbook. Both these facts could explain the difference in assignment.

Is high BLUP correlated to previous crossbreeding between the North Swedish Trotter and the Standardbred?

The North Swedish Trotters used in this study were chosen for their high BLUP values as well as that they should be as unrelated as possible. However, when taking a closer look on the pedigrees of the stallions, there were some commonalities between the horses. The stallion Solo, who was the father of Solatla that was disqualified in the 1950's because of a close resemblance to the Standardbred, was in the pedigree four or five generations back in five of the stallions used here. Ceres E Ulrik, Pavin and Toftejänta were also in the pedigree three to five generations back for five of the horses, some of which had more than one of those horses in their pedigree. This shows that the studbook is relatively young and that the effective population size probably is rather small, thus increasing the risk of genetic drift and selection.

Conclusion

This study showed, as expected, that the North Swedish Trotter was closer to the North Swedish Draught Horse than to the Standardbred. The three breeds were shown to be three separate breeds. Interesting, however, was that the North Swedish Trotter perhaps was not as far from the Standardbred as it should be if it only originated from the North Swedish Draught Horse. To further investigate this more data is needed. At the time of writing genotyping with the help of a SNP-chip (single

nucleotide polymorphism) is being performed. This makes it possible to analyze a very large number of genetic markers simultaneously. Results will be expected sometime in the spring of 2009.

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APPENDIX 1: List of all loci used in the study and their respective chromosome assignment (ECA, *Equus caballus*), and reference. Shaded loci are those that were genotyped again to complement already existing data.

	Locus	ECA	Reference
1	A14	2	Lindgren <i>et al.</i> , 1998
2	A17	26	Lindgren <i>et al.</i> , 1998
3	AHT16	15	Swinburne <i>et al.</i> , 2000
4	AHT17	12	Swinburne <i>et al.</i> , 2000
5	AHT21	1	Swinburne <i>et al.</i> , 2000
6	AHT4	24	Godard <i>et al.</i> , 1998
7	AHT5	8	Shiue <i>et al.</i> , 1999
8	ASB14	8	Breen <i>et al.</i> , 1997
9	ASB17	2	Breen <i>et al.</i> , 1997
10	ASB18	2	Breen <i>et al.</i> , 1997
11	ASB2	15	Breen <i>et al.</i> , 1997
12	ASB22	4	Breen <i>et al.</i> , 1997
13	ASB23	3	Lindgren <i>et al.</i> , 1998
14	ASB41	1	Lear <i>et al.</i> , 1999
15	ASB8	1	Breen <i>et al.</i> , 1997
16	ASB9	10	Breen <i>et al.</i> , 1997
17	B8	15	Marti <i>et al.</i> , 1998
18	CA425	28	
19	COR2	14	Hopman <i>et al.</i> , 1999
20	COR3	8	Hopman <i>et al.</i> , 1999
21	COR7	17	Hopman <i>et al.</i> , 1999
22	COR8	9	Hopman <i>et al.</i> , 1999
23	COR14	15	Hopman <i>et al.</i> , 1999
24	COR16	22	Hopman <i>et al.</i> , 1999
25	COR17	27	Hopman <i>et al.</i> , 1999
26	COR18	25	Hopman <i>et al.</i> , 1999
27	COR20	10	Hopman <i>et al.</i> , 1999
28	COR24	24	Murphie <i>et al.</i> , 1999
29	COR27	29	Murphie <i>et al.</i> , 1999
30	COR31	27	Murphie <i>et al.</i> , 1999
31	COR32	17	Murphie <i>et al.</i> , 1999
32	COR33	3	Murphie <i>et al.</i> , 1999
33	COR38	31	Murphie <i>et al.</i> , 1999
34	COR40	27	Murphie <i>et al.</i> , 1999
35	COR55	23	Ruth <i>et al.</i> , 1999
36	COR56	8	Ruth <i>et al.</i> , 1999
37	COR58	12	Ruth <i>et al.</i> , 1999
38	COR61	24	Tallmadge <i>et al.</i> , 1999
39	COR62	19	Tallmadge <i>et al.</i> , 1999
40	COR69	13	Tallmadge <i>et al.</i> , 1999
41	COR70	6	Tallmadge <i>et al.</i> , 1999
42	COR71	26	Tallmadge <i>et al.</i> , 1999

43	COR73	21	Tallmadge <i>et al.</i> , 1999
44	COR75	15	Tallmadge <i>et al.</i> , 1999
45	COR82	29	Tallmadge <i>et al.</i> , 1999
46	COR88	6	Tallmadge <i>et al.</i> , 1999
47	COR89	4	Tallmadge <i>et al.</i> , 1999
48	COR92	19	Tallmadge <i>et al.</i> , 1999
49	COR96	18	Tallmadge <i>et al.</i> , 1999
50	COR100	1	Tallmadge <i>et al.</i> , 1999
51	EB2E8	26	Shiue <i>et al.</i> , 1999
52	HMS1	15	Bailey <i>et al.</i> , 1995
53	HMS2	10	Bailey <i>et al.</i> , 1995
54	HMS3	9	Bailey <i>et al.</i> , 1995
55	HMS15	1	Godard <i>et al.</i> , 1998
56	HMS47	22	Godard <i>et al.</i> , 1997
57	HMS5	5	Bailey <i>et al.</i> , 1995
58	HMS6	3	Bailey <i>et al.</i> , 1995
59	HMS7	1	Bailey <i>et al.</i> , 1995
60	HTG10	21	Marklund <i>et al.</i> , 1994
61	HTG21	22	Lindgren <i>et al.</i> , 1999
62	HTG3	16	Bailey <i>et al.</i> , 1995
63	HTG4	9	Bailey <i>et al.</i> , 1995
64	HTG6	15	Bailey <i>et al.</i> , 1995
65	HTG7	4	Bailey <i>et al.</i> , 1995
66	I18	16	Lindgren <i>et al.</i> , 1998
67	L12.2	29	Guerin <i>et al.</i> , 1999
68	L15.2	16	Guerin <i>et al.</i> , 1999
69	LEX4	4	Coogle <i>et al.</i> , 1996a
70	LEX7	3	Coogle <i>et al.</i> , 1996a
71	LEX22	x	Coogle <i>et al.</i> , 1996b
72	LEX25	30	Coogle <i>et al.</i> , 1996c
73	LEX36	19	Coogle <i>et al.</i> , 1997
74	LEX37	21	Coogle <i>et al.</i> , 1997
75	LEX54	18	Coogle & Bailey, 1997
76	LEX56	16	Coogle & Bailey, 1997
77	LEX57	3	Coogle & Bailey, 1997
78	LEX71	20	Bailey <i>et al.</i> , 2000
79	LEX73	19	Bailey <i>et al.</i> , 2000
80	LEX74	24	Bailey <i>et al.</i> , 2000
81	NVHEQ29	4	Roed <i>et al.</i> , 1998
82	NVEQ100	1	Roed <i>et al.</i> , 1998
83	NVHEQ70	26	Bjornstad <i>et al.</i> , 2000
84	NVHEQ79	17	Bjornstad <i>et al.</i> , 2000
85	NVHEQ82	6	Bjornstad <i>et al.</i> , 2000
86	SGCV10	12	Godard <i>et al.</i> , 1997
87	SGCV16	21	Godard <i>et al.</i> , 1997
88	SGCV8	12	Godard <i>et al.</i> , 1997
89	TKY1001	6	Tozaki <i>et al.</i> , 2004
90	TKY1175	5	Tozaki <i>et al.</i> , 2004

91	TKY19	18	Kakoi <i>et al.</i> , 1999
92	TKY294	27	Tozaki <i>et al.</i> , 2000
93	TKY297	1	Tozaki <i>et al.</i> , 2000
94	TKY301	23	Tozaki <i>et al.</i> , 2000
95	TKY321	20	Tozaki <i>et al.</i> , 2000
96	TKY333	28	Tozaki <i>et al.</i> , 2001
97	TKY337	4	Tozaki <i>et al.</i> , 2001
98	TKY341	16	Tozaki <i>et al.</i> , 2001
99	TKY343	11	Tozaki <i>et al.</i> , 2001
100	TKY374	1	Tozaki <i>et al.</i> , 2001
101	TKY394	24	Tozaki <i>et al.</i> , 2001
102	TKY404	12	Tozaki <i>et al.</i> , 2004
103	TKY447	3	Tozaki <i>et al.</i> , 2004
104	TKY466	1	Tozaki <i>et al.</i> , 2004
105	TKY471	10	Tozaki <i>et al.</i> , 2004
106	TKY477	20	Tozaki <i>et al.</i> , 2004
107	TKY486	23	Tozaki <i>et al.</i> , 2004
108	TKY532	16	Tozaki <i>et al.</i> , 2004
109	TKY544	5	Tozaki <i>et al.</i> , 2004
110	TKY546	17	Tozaki <i>et al.</i> , 2004
111	TKY551	11	Tozaki <i>et al.</i> , 2004
112	TKY554	22	Tozaki <i>et al.</i> , 2004
113	TKY572	22	Tozaki <i>et al.</i> , 2004
114	TKY573	8	Tozaki <i>et al.</i> , 2004
115	TKY594	13	Tozaki <i>et al.</i> , 2004
116	TKY596	22	Tozaki <i>et al.</i> , 2004
117	TKY613	7	Tozaki <i>et al.</i> , 2004
118	TKY630	11	Tozaki <i>et al.</i> , 2004
119	TKY636	14	Tozaki <i>et al.</i> , 2004
120	TKY693	13	Tozaki <i>et al.</i> , 2004
121	TKY698	4	Tozaki <i>et al.</i> , 2004
122	TKY710	11	Tozaki <i>et al.</i> , 2004
123	TKY711	1	Tozaki <i>et al.</i> , 2004
124	TKY715	29	Tozaki <i>et al.</i> , 2004
125	TKY734	12	Tozaki <i>et al.</i> , 2004
126	TKY741	18	Tozaki <i>et al.</i> , 2004
127	TKY757	7	Tozaki <i>et al.</i> , 2004
128	TKY784	2	Tozaki <i>et al.</i> , 2004
129	TKY792	17	Tozaki <i>et al.</i> , 2004
130	TKY842	2	Tozaki <i>et al.</i> , 2004
131	TKY850	2	Tozaki <i>et al.</i> , 2004
132	TKY867	10	Tozaki <i>et al.</i> , 2004
133	TKY930	14	Tozaki <i>et al.</i> , 2004
134	UCDEQ437	3	Eggleston-Stott <i>et al.</i> , 1997
135	UCDEQ467	24	Eggleston-Stott <i>et al.</i> , 1997
136	UCDEQ487	1	Eggleston-Stott <i>et al.</i> , 1997
137	UMO37	7	George <i>et al.</i> , 1998
138	UMO38	x	George <i>et al.</i> , 1998

139	UM32	14	Swinburne <i>et al.</i> , 2000
140	VHL47	13	van Haeringen <i>et al.</i> , 1998a
141	VHL20	30	Bailey <i>et al.</i> , 1995
142	VIASH34	1	Ewen & Matthews, 1994
143	TKY450	8	Tozaki <i>et al.</i> , 2004
144	TKY489	5	Tozaki <i>et al.</i> , 2004

APPENDIX 2: Brief instructions on how STRUCTURE 2.2 was run.

The in-file was made in Excel and saved as a text file with data shown in a matrix. Each individual was presented on two rows where the first row showed the first three numbers (the first allele) of the locus and the second row (the second allele) showed the last three numbers of the locus. Each locus was thus presented in one column but over two rows. Names of loci were not included in the in-file. The given population, or breed, was defined for each individual in one column. The in-file thus ended up as a matrix with 145 columns and 60 rows.

Next, a new project was started which was named and directory and data files were selected. As missing data value -9 was used and the box for putative population origin for each individual was checked. Before running the project a new parameter set was established. The burning period was set to 10 000 and the number of MCMC repeats was set to 100 000. The admixture model was used and allele frequencies correlated. The project was then run from the parameter set and assumed number of populations, K , was set to three.

APPENDIX 3. List of individual values for expected, H_e , and observed heterozygosity, H_o . All n is the total number of alleles for each locus and n for the three breeds is the number of alleles for that locus for each breed.

<i>Microsatellite loci</i>	All	North Swedish Draught			Standardbred			North Swedish Trotter		
	<i>n</i>	<i>n</i>	<i>He</i>	<i>Ho</i>	<i>n</i>	<i>He</i>	<i>Ho</i>	<i>n</i>	<i>He</i>	<i>Ho</i>
A14	13.00	6.00	0.734	0.875	7.00	0.728	0.667	6.00	0.792	0.667
A17	8.00	5.00	0.685	0.600	4.00	0.648	0.667	6.00	0.735	0.429
AHT16	2.00	1.00	0.000	0.000	2.00	0.095	0.100	1.00	0.000	0.000
AHT17	10.00	5.00	0.660	0.700	6.00	0.688	0.750	7.00	0.805	0.625
AHT21	8.00	2.00	0.480	0.200	6.00	0.790	0.889	6.00	0.758	0.750
AHT4	10.00	6.00	0.850	0.900	6.00	0.835	1.000	6.00	0.845	1.000
AHT5	8.00	5.00	0.845	1.000	4.00	0.785	1.000	5.00	0.820	1.000
ASB14	6.00	5.00	0.734	0.875	2.00	0.198	0.222	3.00	0.648	0.500
ASB17	14.00	9.00	0.840	0.900	9.00	0.858	0.889	5.00	0.714	0.714
ASB18	10.00	6.00	0.716	0.778	4.00	0.500	0.556	4.00	0.633	0.875
ASB2	8.00	6.00	0.815	1.000	6.00	0.810	1.000	4.00	0.800	1.000
ASB22	7.00	7.00	0.815	0.667	4.00	0.531	0.571	6.00	0.789	0.875
ASB23	7.00	4.00	0.625	0.600	6.00	0.630	0.556	4.00	0.633	0.625
ASB41	6.00	5.00	0.636	0.778	2.00	0.278	0.333	4.00	0.514	0.500
ASB8	6.00	4.00	0.512	0.667	4.00	0.667	0.889	4.00	0.704	0.857
ASB9	1.00	1.00	0.000	0.000	1.00	0.000	0.000	1.00	0.000	0.000
B8	4.00	3.00	0.405	0.500	3.00	0.398	0.250	2.00	0.490	0.857
CA425	7.00	4.00	0.780	1.000	7.00	0.865	1.000	5.00	0.840	1.000
COR2	7.00	3.00	0.568	0.778	4.00	0.599	0.667	6.00	0.776	0.714
COR3	6.00	5.00	0.734	0.875	4.00	0.673	0.778	4.00	0.694	0.857
COR7	7.00	4.00	0.720	0.600	4.00	0.599	0.556	5.00	0.704	0.714
COR8	12.00	8.00	0.815	0.889	6.00	0.720	0.800	7.00	0.803	0.778
COR14	7.00	4.00	0.675	0.600	6.00	0.765	0.889	3.00	0.561	0.571
COR16	6.00	3.00	0.580	0.900	4.00	0.451	0.444	2.00	0.219	0.250
COR17	7.00	5.00	0.680	0.700	5.00	0.784	0.778	5.00	0.750	0.625
COR18	8.00	6.00	0.741	0.667	4.00	0.727	0.875	5.00	0.740	0.600
COR20	7.00	5.00	0.742	0.875	6.00	0.766	0.875	4.00	0.660	1.000
COR24	5.00	3.00	0.585	0.600	5.00	0.753	0.778	5.00	0.664	0.750
COR27	8.00	6.00	0.770	0.700	4.00	0.562	0.778	6.00	0.758	0.750
COR31	6.00	5.00	0.640	0.400	4.00	0.667	0.556	4.00	0.680	0.375
COR32	3.00	3.00	0.320	0.125	3.00	0.426	0.111	3.00	0.340	0.200
COR33	8.00	5.00	0.624	0.333	5.00	0.704	0.667	6.00	0.578	0.625
COR38	4.00	4.00	0.345	0.300	1.00	0.000	0.000	2.00	0.117	0.125
COR40	9.00	4.00	0.562	0.556	4.00	0.648	0.625	7.00	0.766	0.750
COR55	7.00	5.00	0.480	0.500	4.00	0.667	0.889	4.00	0.672	0.750
COR56	8.00	5.00	0.785	0.900	5.00	0.654	0.889	5.00	0.773	0.750
COR58	9.00	6.00	0.741	0.667	4.00	0.444	0.444	3.00	0.622	0.714
COR61	8.00	7.00	0.830	0.900	5.00	0.679	1.000	4.00	0.725	0.571
COR62	9.00	6.00	0.796	0.857	5.00	0.735	0.857	5.00	0.720	0.600
COR69	7.00	6.00	0.600	0.700	3.00	0.508	0.750	5.00	0.755	0.857
COR70	16.00	6.00	0.766	0.625	8.00	0.805	0.750	8.00	0.806	0.857

COR71	5.00	4.00	0.691	0.778	4.00	0.691	0.889	4.00	0.664	0.625
COR73	8.00	4.00	0.617	0.667	6.00	0.734	0.375	4.00	0.459	0.571
COR75	9.00	5.00	0.715	0.400	6.00	0.765	0.889	3.00	0.541	0.571
COR82	8.00	7.00	0.778	0.667	5.00	0.625	0.625	6.00	0.735	0.857
COR88	3.00	2.00	0.444	0.000	1.00	0.000	0.000	3.00	0.255	0.286
COR89	12.00	8.00	0.827	0.857	5.00	0.580	0.667	6.00	0.700	0.800
COR92	6.00	6.00	0.745	0.800	4.00	0.661	0.778	6.00	0.789	0.875
COR96	7.00	4.00	0.595	0.400	3.00	0.624	0.778	5.00	0.656	0.500
COR100	8.00	4.00	0.565	0.700	5.00	0.630	0.667	5.00	0.680	1.000
EB2E8	6.00	5.00	0.820	0.900	5.00	0.840	1.000	3.00	0.719	1.000
HMS1	6.00	4.00	0.730	0.900	4.00	0.840	1.000	4.00	0.719	1.000
HMS2	7.00	3.00	0.660	0.900	6.00	0.885	1.000	4.00	0.740	1.000
HMS3	8.00	5.00	0.840	0.700	6.00	0.835	1.000	6.00	0.835	0.900
HMS15	9.00	5.00	0.725	0.900	4.00	0.656	0.250	5.00	0.742	0.625
HMS47	6.00	4.00	0.377	0.222	4.00	0.667	0.667	4.00	0.484	0.250
HMS5	3.00	3.00	0.705	1.000	3.00	0.660	1.000	3.00	0.655	1.000
HMS6	6.00	6.00	0.820	1.000	5.00	0.803	1.000	6.00	0.835	1.000
HMS7	5.00	4.00	0.750	1.000	4.00	0.730	1.000	3.00	0.690	1.000
HTG10	7.00	6.00	0.810	1.000	5.00	0.790	1.000	4.00	0.770	1.000
HTG21	5.00	4.00	0.530	0.400	4.00	0.691	0.889	3.00	0.439	0.571
HTG3	6.00	4.00	0.800	1.000	5.00	0.780	1.000	5.00	0.755	1.000
HTG4	6.00	4.00	0.795	1.000	5.00	0.755	1.000	5.00	0.845	1.000
HTG6	4.00	2.00	0.605	1.000	4.00	0.715	1.000	3.00	0.640	1.000
HTG7	5.00	5.00	0.725	1.000	2.00	0.545	1.000	0.63	1.000	0.563
I18	8.00	4.00	0.691	0.556	6.00	0.795	0.700	5.00	0.622	0.857
L12.2	10.00	3.00	0.290	0.333	6.00	0.790	0.889	5.00	0.570	0.500
L15.2	7.00	4.00	0.615	0.900	5.00	0.664	0.875	4.00	0.672	0.875
LEX4	10.00	5.00	0.773	0.750	3.00	0.364	0.111	5.00	0.760	0.800
LEX7	6.00	4.00	0.681	0.833	4.00	0.563	0.750	5.00	0.740	0.600
LEX22	6.00	4.00	0.691	0.000	6.00	0.781	0.000	0.47	0.000	0.000
LEX25	6.00	5.00	0.765	0.889	4.00	0.602	0.625	5.00	0.750	0.375
LEX36	9.00	5.00	0.760	0.600	6.00	0.773	0.750	4.00	0.672	0.875
LEX37	6.00	4.00	0.415	0.400	2.00	0.105	0.111	4.00	0.643	0.571
LEX54	9.00	6.00	0.694	0.714	2.00	0.198	0.222	7.00	0.837	0.571
LEX56	8.00	6.00	0.759	1.000	5.00	0.735	1.000	4.00	0.562	0.556
LEX57	7.00	4.00	0.617	0.625	4.00	0.664	0.625	7.00	0.755	0.714
LEX71	7.00	5.00	0.645	0.800	3.00	0.512	0.667	5.00	0.773	0.750
LEX73	8.00	4.00	0.635	0.600	4.00	0.636	0.778	5.00	0.641	0.375
LEX74	13.00	8.00	0.784	0.556	7.00	0.741	0.889	5.00	0.722	0.500
NVHEQ29	8.00	5.00	0.705	0.500	5.00	0.568	0.556	6.00	0.805	0.800
NVEQ100	10.00	7.00	0.815	0.556	4.00	0.735	0.571	3.00	0.569	0.333
NVHEQ70	5.00	4.00	0.562	0.667	4.00	0.636	0.556	4.00	0.633	0.750
NVHEQ79	11.00	7.00	0.789	0.625	6.00	0.753	0.667	5.00	0.653	0.857
NVHEQ82	6.00	5.00	0.645	0.800	4.00	0.636	0.667	6.00	0.796	0.857
SGCV10	6.00	5.00	0.792	1.000	4.00	0.704	0.714	5.00	0.764	0.833
SGCV16	5.00	3.00	0.185	0.200	4.00	0.512	0.444	2.00	0.117	0.125
SGCV8	9.00	6.00	0.690	0.700	5.00	0.679	0.889	8.00	0.859	1.000
TKY1001	7.00	3.00	0.520	0.429	5.00	0.664	0.500	5.00	0.680	0.700
TKY1175	3.00	3.00	0.602	0.714	2.00	0.337	0.143	3.00	0.541	0.714

TKY19	7.00	7.00	0.830	0.800	3.00	0.624	0.889	7.00	0.815	0.778
TKY294	7.00	4.00	0.780	1.000	6.00	0.810	1.000	6.00	0.830	1.000
TKY297	10.00	7.00	0.820	1.000	5.00	0.800	1.000	7.00	0.870	1.000
TKY301	9.00	6.00	0.800	1.000	7.00	0.790	1.000	8.00	0.840	1.000
TKY321	7.00	4.00	0.735	1.000	6.00	0.845	1.000	3.00	0.730	1.000
TKY333	12.00	8.00	0.850	1.000	6.00	0.835	1.000	9.00	0.830	0.900
TKY337	6.00	6.00	0.805	1.000	5.00	0.860	1.000	4.00	0.820	1.000
TKY341	8.00	6.00	0.790	0.800	5.00	0.747	0.556	4.00	0.708	0.833
TKY343	11.00	5.00	0.725	1.000	4.00	0.593	0.667	5.00	0.525	0.556
TKY374	8.00	6.00	0.750	0.700	5.00	0.673	0.667	5.00	0.710	0.800
TKY394	8.00	6.00	0.845	1.000	5.00	0.765	1.000	5.00	0.780	1.000
TKY404	8.00	6.00	0.710	0.800	5.00	0.704	0.889	2.00	0.500	0.556
TKY447	6.00	4.00	0.525	0.500	3.00	0.520	0.714	4.00	0.624	0.667
TKY466	5.00	4.00	0.648	0.500	4.00	0.636	0.778	4.00	0.612	0.857
TKY471	4.00	3.00	0.643	0.857	4.00	0.655	0.500	4.00	0.583	0.833
TKY477	9.00	6.00	0.741	0.667	6.00	0.790	0.667	4.00	0.684	1.000
TKY486	10.00	4.00	0.710	0.667	6.00	0.736	0.833	5.00	0.760	0.800
TKY532	10.00	6.00	0.785	0.600	6.00	0.755	1.000	5.00	0.656	0.750
TKY544	8.00	5.00	0.719	0.750	4.00	0.648	0.625	4.00	0.653	0.167
TKY546	3.00	3.00	0.545	0.500	2.00	0.455	0.500	2.00	0.219	0.250
TKY551	3.00	3.00	0.568	0.556	3.00	0.461	0.500	1.00	0.000	0.000
TKY554	4.00	2.00	0.444	0.667	2.00	0.305	0.375	4.00	0.531	0.571
TKY572	5.00	4.00	0.685	0.900	4.00	0.296	0.333	3.00	0.494	0.333
TKY573	6.00	5.00	0.734	0.875	3.00	0.571	0.714	3.00	0.557	0.667
TKY594	4.00	3.00	0.477	0.250	4.00	0.611	0.889	3.00	0.570	0.500
TKY596	5.00	2.00	0.401	0.556	4.00	0.578	0.750	4.00	0.708	0.833
TKY613	6.00	5.00	0.784	1.000	6.00	0.821	0.889	4.00	0.555	0.625
TKY630	8.00	4.00	0.655	0.700	4.00	0.635	0.700	6.00	0.790	0.778
TKY636	9.00	5.00	0.753	0.889	4.00	0.680	0.876	6.00	0.716	0.889
TKY693	10.00	6.00	0.590	0.400	4.00	0.512	0.556	5.00	0.698	0.556
TKY698	7.00	5.00	0.765	0.900	5.00	0.570	0.750	4.00	0.514	0.500
TKY710	4.00	3.00	0.580	0.200	4.00	0.698	0.889	4.00	0.685	0.556
TKY711	5.00	4.00	0.565	0.700	4.00	0.568	0.444	3.00	0.569	0.667
TKY715	7.00	4.00	0.562	0.778	3.00	0.625	0.625	7.00	0.648	0.500
TKY734	6.00	6.00	0.803	0.889	3.00	0.357	0.286	3.00	0.653	0.833
TKY741	9.00	4.00	0.722	0.667	5.00	0.655	0.856	6.00	0.778	0.667
TKY757	11.00	6.00	0.650	0.700	5.00	0.625	0.750	6.00	0.686	0.500
TKY784	8.00	8.00	0.775	0.800	4.00	0.296	0.333	3.00	0.586	0.667
TKY792	7.00	4.00	0.691	0.889	3.00	0.571	0.857	5.00	0.457	0.333
TKY842	9.00	6.00	0.770	0.800	4.00	0.680	0.876	6.00	0.720	0.750
TKY850	8.00	4.00	0.655	0.800	4.00	0.661	0.667	6.00	0.690	0.800
TKY867	8.00	4.00	0.525	0.500	3.00	0.520	0.714	6.00	0.680	0.600
TKY930	9.00	6.00	0.755	0.857	5.00	0.570	0.755	5.00	0.742	0.550
UCDEQ437	6.00	4.00	0.346	0.400	5.00	0.710	0.778	4.00	0.672	0.625
UCDEQ467	7.00	3.00	0.460	0.600	4.00	0.610	0.700	5.00	0.626	0.750
UCDEQ487	5.00	4.00	0.667	1.000	4.00	0.719	0.755	3.00	0.556	0.571
UMO37	5.00	5.00	0.704	0.889	3.00	0.370	0.444	3.00	0.500	0.714
UMO38	6.00	5.00	0.766	0.700	5.00	0.680	0.376	3.00	0.612	0.857
UM32	5.00	5.00	0.810	1.000	3.00	0.664	1.000	4.00	0.781	1.000

VHL47	5.00	5.00	0.700	0.700	4.00	0.716	0.778	2.00	0.408	0.571
VHL20	9.00	7.00	0.855	1.000	5.00	0.830	1.000	8.00	0.825	1.000
VIASH34	4.00	4.00	0.653	0.833	3.00	0.320	0.375	3.00	0.255	0.286
TKY450	8.00	5.00	0.755	1.000	7.00	0.789	0.875	5.00	0.780	0.800
TKY489	4.00	3.00	0.540	0.600	3.00	0.561	0.714	4.00	0.563	0.750
Average	7.17	4.75	0.666	0.709	4.40	0.627	0.699	4.51	0.649	0.692