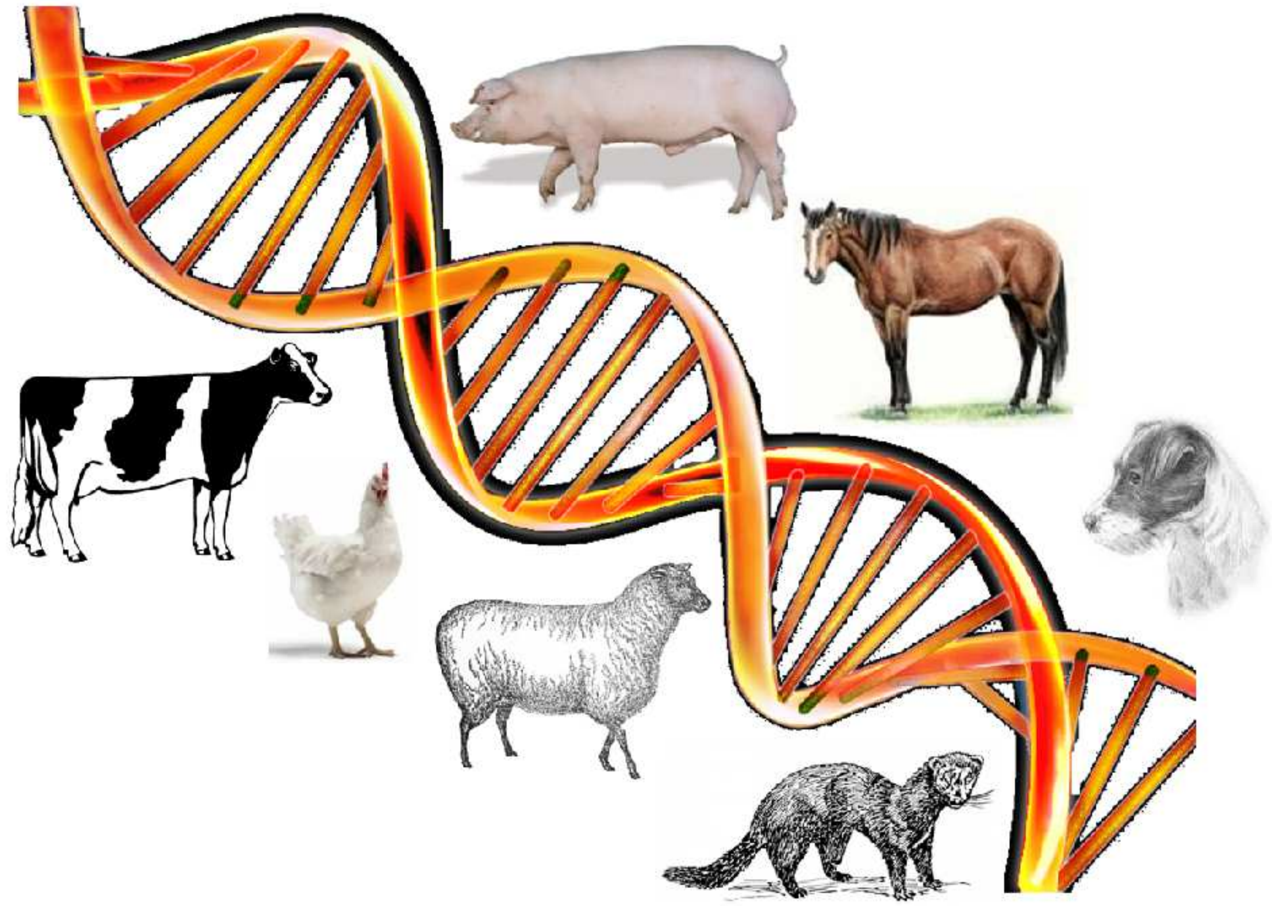
Applied Animal Breeding for Different Species

- with a focus on Danish circumstances



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Preface

These course notes were written as a supplement to Understanding Animal Breeding by R. M. Bourdon (2nd edition, Prentice Hall), which is an introduction to general breeding theory applying to all animal species. Although the basic principles of inheritance and breeding are the same for all animals, the implementation of breeding schemes differs considerably from species to species. Reasons for this include differences in reproductive capacity, in the potential to record traits of interest, and in available resources for research and implementation. Hence, these notes attempt to describe applied breeding methods for different domestic animal species as currently implemented. Some information presented here may be out of date by the time it is read, as techniques in applied breeding are constantly evolving. The descriptions focus on Danish circumstances because the notes are intended for Danish students. However, an attempt has been made to include international perspectives where relevant — not least because breeding is becoming more and more international, but also because students are expected to deal with international challenges in their future careers. While practices can vary from country to country, they are typically much more similar here than they are across species. There are individual chapters on the following species (or groups of species): pigs, dairy cattle, poultry, fur animals, sheep, horses and dogs. As far as possible the chapters has been structured the same way to easy across-species comparisons. Unfortunately, owing to time constraints, other important species are not dealt with in these notes. I greatly appreciate all the help I have been given by the (co)authors of the various chapters, and the helpful comments made by Gert Aamand, Lars Nielsen (dairy cattle), Niels Enggaard Hansen, Bente Krogh Hansen and Jesper Clausen (fur animals).

Thomas Mark

Frederiksberg, February 2011

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Pig Breeding

Thomas Mark & Tage Ostersen

Introduction

Pigs are used mainly for producing human foods. Meat cuts are the main interest, but other products derived from the carcass, such as legs and noses (e.g. for Chinese market), are used for human consumption. Secondary uses of pigs include manure production and the fulfilment of cultural needs. In medical research, pigs are also used as models of humans. Pigs are kept in a broad spectrum of production environments around the world, but in Denmark the vast majority are kept in intensive housing conditions with a controlled climate; a minority of Danish pigs are kept outside in free range environments.

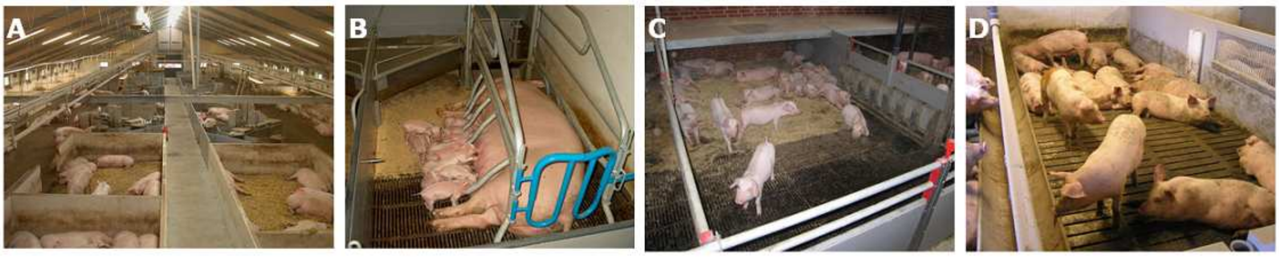

Figure 1. Pictures of typical housing facilities for different groups of Danish production pigs (A. Pregnant sows, B. Farrowing sows, C. Piglets, D. Slaughter pigs. Photos by J. Vinther, N. P. Nielsen, A. L. Riis and T. L. Jensen, respectively)

Denmark is among the world's largest pig producers. In 2009, 19.3 million pigs were slaughtered in Denmark, which corresponds to 2 million tonnes of meat. Worldwide, about 93 million tonnes of pig meat was generated by slaughter in 2009. In Denmark, 94% of the meat produced in 2009 was exported; and Germany (30% of that meat), United Kingdom (15%), Japan (7%) and China (7%) were among the larger importers of Danish pig meat (Landbrug og Fødevarer, 2010).

Artificial insemination (AI) with fresh (non-frozen) semen is used in most matings. Boars can produce about 50 doses of semen per week, and this allows them to be intensively selected. Purebred Landrace, Yorkshire and Duroc sows farrow 15.3, 15.3 and 9.8 piglets per litter on average. Gilts reach sexual maturity at 6–7 months of age, and their average gestation length is 116 days.

Breeds

Danish pig production is based mainly on three breeds: Duroc, Landrace and Yorkshire (Fig. 2). Duroc is used as a terminal sire on Landrace x Yorkshire (LY) sows to produce crossbred pigs for Danish production herds. Other countries use breeds with the same names and similar origin as these 'Danish' breeds, but their populations differ as the result of, among things, different breeding goals and the restricted exchange of genetic material. Hampshire, Piétrain and Berkshire are also used in some countries, and locally other breeds continue to have some commercial influence. China, the world's largest swine industry, has been based on roughly six types of pig, defined by geographical location and origin. However, a rapid transition is taking place in China to US and/or European breeds, and now Piétrain, Duroc, Landrace and Yorkshire are the most commonly used breeds in modern cross-breeding systems. Durocs were imported from North America to Denmark in the late 1970s. Besides its high growth capacity, good carcass traits and high feed efficiency, the breed is recognized by its red-brown colour. Yorkshire and Landrace are both white. They are known for their maternal qualities (i.e. they have large litters and nurse their piglets well).

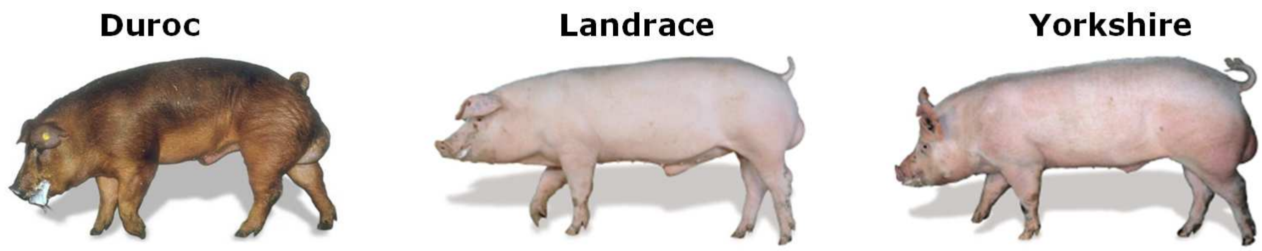

Figure 2. The three breeds used in Danish pig breeding

Breeding Goal

The breeding goal is to breed pigs that will generate the highest possible economic return for commercial pig producers over the coming 5–10 years. This breeding goal is decided by commercial pig producers with the guidance of the Breeding & Genetics section at the Danish Agricultural and Food Council. Economic values for most traits are based on a bioeconomic model. This model simulates incomes and costs of each trait in a 'future' production herd; it can be amended to reflect political concerns. The breeding goal is different for paternal (Duroc) and maternal (Landrace, Yorkshire) breeds (Fig. 3).

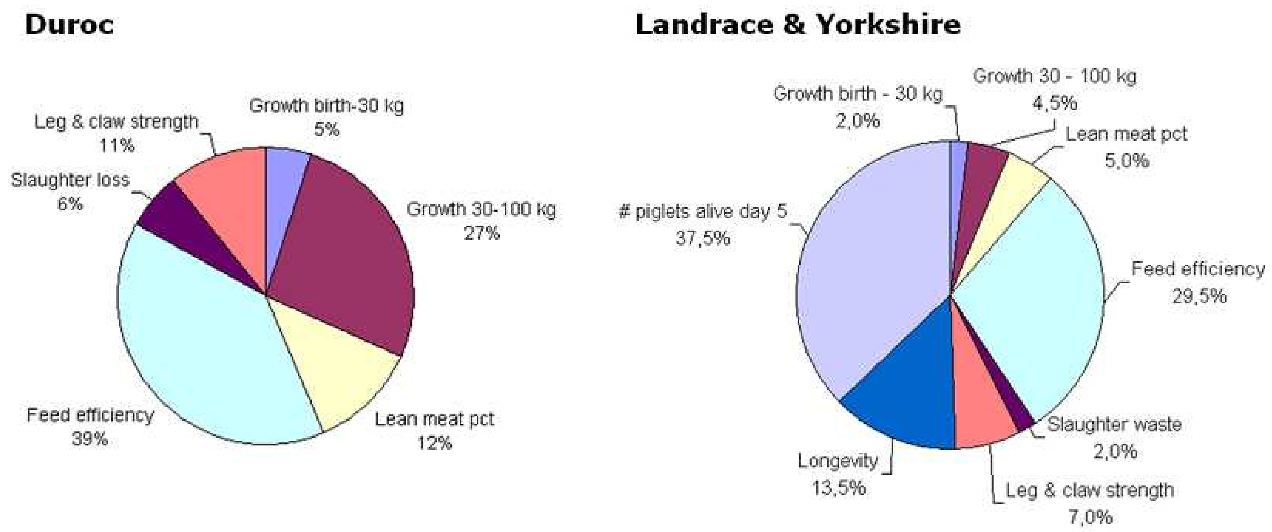

Figure 3. Expected genetic progress for paternal (Duroc) and maternal (Landrace & Yorkshire) breeds in the Danish pig breeding programme. Expected genetic progress for each trait is given in monetary units relative to the total expected economic progress for the total-merit index.

Longevity is defined by whether or not purebred sows in multiplier herds are mated for their 2nd litter. Meat quality is not considered in the breeding goals of Danish pig breeds. In Iberian pigs, however, the percentage of oleic acid is included as the main criterion qualifying products.

Genetic Evaluation and Parameters

Multiple-trait animal models are used in the genetic evaluation of groups of 2–4 traits. For instance, estimated breeding values (EBVs) for feed efficiency, the two growth traits and lean meat percentage are calculated using a four-trait model. Although genetic correlations are relatively small this is especially advantageous for feed efficiency, because animals without records on feed efficiency, but with records on one or more of the other traits, obtain EBVs that are based on correlated information.

The explanatory effects used in the genetic evaluations to account for environmental effects differ from trait to trait. Typical effects are sex, herd-year-month of registration, common environment for litters, common environment effect for the housing group of pigs, and weight of the animal at the onset of the registration period (e.g. growth 30–100 kg). The bivariate model for number of piglets alive after day 5 and litter size also includes effects of parity of sow, the sow's age at 1st farrowing (1st parity only), farrowing interval (later parities only) and type of fertilization (AI or natural).

The parameters used in genetic evaluation and in the breeding programme for Landrace pigs are summarized below in Table 1. The heritabilities and correlations are similar for Duroc and Yorkshire, whereas variances in some traits differ. Strength of legs and claws, number of pigs alive after day 5, and sow longevity have low heritability (0.08–0.17). The last two traits are not evaluated for Duroc.

Table 1. Genetic parameters for Landrace pigs used for genetic evaluations

	A	B	C	D	E	F	G	H
h^2	0.29	0.33	0.44	0.12	0.31	0.08	0.39	0.17
σ^2_a	214	2192	0.542	0.095	0.0074	0.788	0.912	0.028
Genetic (above diagonal) and residual (below diagonal) correlations:[1]								
A. Growth, birth to 30 kg (g/day)		0.33	-0.04	-	-0.20	-	-	-
B. Growth, 30-100 kg (g/day)	0.10		0.48	-	-0.35	-	-	-0.25
C. Lean meat percentage (%)	0.05	-0.16		-	-0.28	-	-	-0.11
D. Strength of legs and claws (points)	-	-	-		-	-	-	0.14
E. Feed efficiency (FE/kg gain)	-0.04	-0.49	-0.08	-		-	-	-
F. No. piglets alive after day 5 (#/litter)	-	-	-	-	-		-	-
G. Slaughter loss (kg)	-	-	-	-	-	-		-
H. Sow longevity (%)	-	0.09	0	0.05	-	-	-	

[1]Correlations are unknown for some trait combinations; this is indicated by '-'

Genetic correlations between male (e.g. growth, feed efficiency) and female traits (e.g. no. piglets alive after day 5, sow longevity) tracked in the Danish system are not estimated. Research on foreign pig populations suggests that the genetic correlations between growth and reproductive traits are either unfavourable (e.g. Holm et al., 2004) or close to zero (e.g. Arango et al., 2005).

Organization and Breeding Programme

Danish pig breeding is organized around a classical breeding pyramid (see Fig. 4). In 2010 the Danish pig population consisted of 32 breeding herds (1785, 2210 and 2717 Duroc, Yorkshire and Landrace sows, respectively), 153 multiplier herds (69 700 purebred sows) and 2601 production herds with 1.1 million crossbred sows. There is some overlap between the figures, as 29 breeding herds are also multiplier herds.

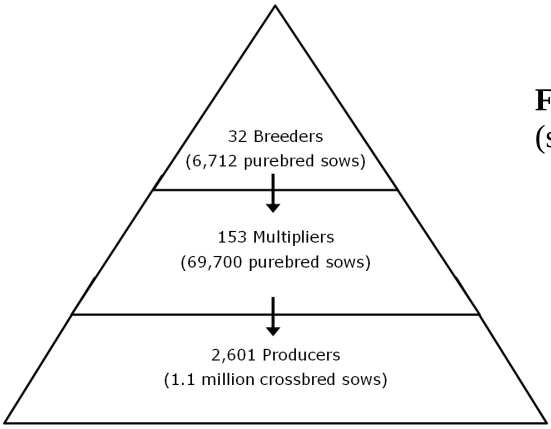

Figure 4. Pyramid structure of Danish pig sector (statistics from 2009-10; Danish Pig Research Centre)

The breeding herds form a closed nucleus with no imports from lower tiers in the pyramid or foreign populations. Thus it is only selection and mating decisions made in the breeding herds that influence the additive genetic trends in the population. The current average genetic level in production herds corresponds approximately to the average genetic level observed in the breeding herds 1–2 generations ago. (Transmission of genes takes 1 and 2–3 generations for boars and sows, respectively.)

Breeders send their best boars to AI-stations and also sell approximately 1000 (mainly Duroc) boars per year to production herds. Purebred females are sold to multiplier herds and, in some cases, directly to production herds. Hence, breeders successfully breeding superior pigs earn more money than their less successful competitors. This is an important motivation for breeders to do their best when they record breeding goal traits, selecting animals with the best EBVs and ensuring optimal matings.

The main function of multiplier herds is to facilitate the transmission of genetic progress made in breeding herds to production herds. In practice, this means producing crossbred females (LY) that are sold to production herds. Multiplier herds receive purebred Landrace and Yorkshire females from breeding herds.

Breeding decisions in production herds are not relevant to future generations of the pig population. Such herds exist primarily for the production of pigs for slaughter. As the vast majority of pigs are raised in production herds, the breeding goal should reflect the circumstances in production herds, and ideally performance measures of breeding animals should be carried out in similar production environments.

Most traits are recorded in the purebred breeding herds. However, feed efficiency is recorded at the test station ‘Bøgildgaard’ and not in individual herds. The number of piglets alive per litter is recorded in multiplier herds as well as in breeding herds to provide sufficient accuracy of breeding values (trait only expressed by sows and low heritability). Slaughter loss is only recorded for slaughtered animals, which makes it impossible to have own records on active breeding animals. The remaining traits are recorded on most pigs in breeding herds — only approximately 25% of the pigs do not have their performance recorded, and this is due mainly to death, disease or experimental discrepancies.

Table 2 shows the approximate proportion of tested pigs that are used for pure-breeding. Selection intensities are substantially higher for boars than gilts as a consequence of AI being used. These intensities are lower for Duroc as compared with the maternal breeds as a result of Duroc’s smaller average litter size, smaller population, and because some Duroc boars are used for both breeding and production herds. The use of selected boars varies substantially (i.e. the number of matings per boar ranges from 1–60).

Table 2. Percentage of tested pigs that are used for pure-breeding

	Boars	Gilts
Duroc	1.6	25
Landrace	1.0	16
Yorkshire	1.0	16

Inbreeding only concerns breeding herds (i.e. purebred pigs) and is controlled by imposing an upper limit of 50–60 matings for a single boar, depending on the breed. Furthermore, a maximum of 40 half- and 2 full-brothers are accepted at the ‘Bøgildgaard’ test station for Yorkshire and Landrace, whereas a maximum of 100 half- and 3 full-brothers are accepted for Durocs. Breeders decide which matings to arrange on the basis of these limitations. Limiting the use of each boar is easy enough in practice, but it is not an optimal way of controlling inbreeding since it does not account for relationships among boars and their breeding values. Therefore, The Danish Agricultural & Food Council’s Pig Research Centre is working on implementing optimum contribution selection of boars (Bendtsen, 2008).

Genomic EBVs based on a 62K SNP chip are currently being developed for all evaluated traits. They are expected to have the greatest impact on longevity, litter size and feed efficiency, where accurate EBVs are not available for young selection candidates. Conversely, they are expected to have little impact on the remaining evaluated traits. Potentially, genomic EBVs will also be developed for health traits that are not being evaluated today. Furthermore, genomic EBVs permit the collection of data on crossbred sows — and the subsequent use of this information, in connection with purebred animals. This helps to overcome problems with genotype by environment interactions and gene expression differences between pure and crossbred pigs due to different background genetics.

Examples of Genetic Trends

Favourable genetic trends for growth, feed efficiency and number of piglets alive at day 5 are shown in Fig. 5. Duroc has made greater genetic improvements in growth and feed efficiency than Landrace and Yorkshire. This can be explained by the higher relative emphasis on these traits in the breeding goal and the larger number of animals with records for feed efficiency. Genetic progress has been lower in Yorkshire than in Landrace for these three key traits; this could be due to the former's smaller population size, small differences in genetic variance or chance. On the other hand, Yorkshire has improved more than Landrace in lean meat percentage over the same period (results not shown).

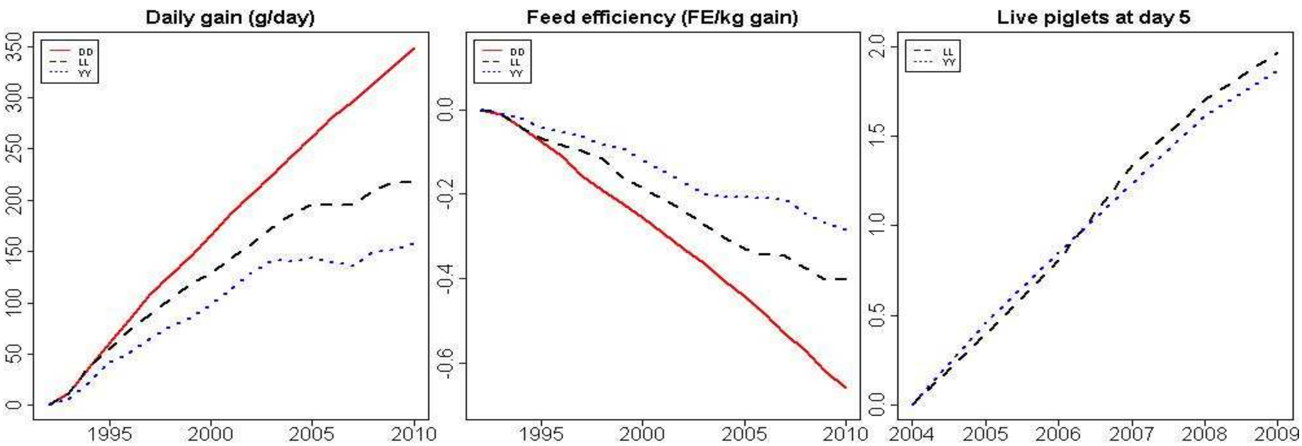

Figure 5. Genetic trends for selected traits. Graphs show average EBV as function of birth year for Duroc (red solid lines), Landrace (black dashed lines) and Yorkshire (blue dotted lines).

References and Further Information

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Dairy Cattle Breeding

Thomas Mark

Introduction

Milk production is the main purpose of dairy cattle production. The ideal cow will have a high milk yield; the milk should have a certain quality (e.g. protein and fat content, low somatic cell-count) and the costs of milk production should be low. A secondary benefit of dairy cattle farming is beef production, although this is not valued in the breeding goals of all breeds. Cattle may also be used for nature conservation, their skin for leather, their bones for various tools, and in some cultures cattle are important for cultural or religious (e.g. Hindu) reasons. Cattle are able to convert inexpensive roughage that cannot be used directly as human food into human food. However, dairy cattle feed in western countries also contains high concentrations of grain, and this is of concern to some people. Other public concerns about cattle include their welfare and carbon-gas emissions.

Dairy cattle are kept in a broad range of environments from low-input pasture to high-input tie-stalls or free-stalls (Fig. 1). The typical Danish dairy herd a couple of decades ago was tie-stalled and numbered less than 50 cows. Today most cows in Denmark are housed in free-stalls in herds of more than 100 cows. At the same time automatic milking systems are replacing more labour intensive parlours in many north-western European countries where there are high minimum wages. Large herds, where animals receive homogeneous management within the herd, make it easier to correct for non-genetic effects in genetic evaluations; they are therefore beneficial for efficient breeding.

Figure 1. Examples of cow environments: A) Danish free-stall, B) Grassing in New Zealand, C) Low-input system in India

About 1.3 billion (i.e. $\times 10^9$) cattle are spread around the globe, if we include both dairy and beef, and this number has been fairly constant for the past few decades (FAO, 2008). In Denmark and other European countries the number of dairy cows has decreased over the past few decades, but the amount of milk being produced has been fairly constant due to a steady increase in milk yield per cow.

The reproductive rate of bulls is high by nature, but can be made extremely high through the cryopreservation of semen and artificial insemination (AI). Hence, a few elite bulls are used in several countries and these have sired several hundred thousand offspring worldwide. By contrast, the reproductive rate of females is low. A cow can have its first calf at around 2 years of age and will on average have just one calf a year hereafter. However, heifers and cows can be super-ovulated using hormones to produce more embryos (around 5 to 6 transferable embryos on average per flush, but variability is high). These embryos can subsequently be flushed and transferred to recipient cows that carry the pregnancy to term. This technique is often used with elite cows to increase their reproductive capacity. It is also possible to separate 'male' and 'female' sperm cells so that the sex of the offspring can be chosen with an accuracy of over 90%.

Figure 2. Semen collection at VikingGenetics. The widespread use of artificial insemination together with sperm sexing enables strong selection of bulls and ensures that a small number of elite bulls sire hundreds of thousands of daughters worldwide.

Breeds

In all 269 cattle breeds are described at http://www.ansi.okstate.edu/breeds (including dairy, beef and dual purpose breeds). However, in western countries with developed dairy production there are fewer than 10 principal international breeds. Here the Holstein population is by far the largest, followed by Simmental, Red Dairy Cattle (RDC), Jersey and Brown Swiss. A great deal of genetic material is exchanged among countries (primarily via semen), so distinguishing between 'national breeds' makes little sense. For instance, many different North American Holstein bulls have been used for decades, and the proportion of genes that can now be traced to original Danish Black and White Cattle (SDM) was estimated at 1.6% in Danish Holstein calves born in 2009. This upgrading process has been termed 'Holsteinization'; it has occurred in many countries.

Holsteins yield large quantities of milk in high-input production environments; they have udders that are well suited to modern milking systems. However, they are considered less robust in extensive or stressful production environments. They are present in all of the main dairy countries. Simmental was originally a dual purpose breed, but today separate lines focus on either beef or milk production. Milking Simmentals are very popular in central Europe and especially in mountainous regions. Red Dairy Cattle are popular in Nordic countries. A relatively strong emphasis has been placed on functional traits such as health and fertility in their breeding goal. Jerseys are a smaller breed and Jersey milk carries a relatively high concentration of fat and protein. The largest Jersey populations are found in New Zealand, the USA and Denmark. In Denmark there are 590 thousand dairy cows (Danmarks Statistik, 2010); most are Holsteins (72%), followed by Jerseys (12%) and Red Dairy Cattle (RDC; 8%).

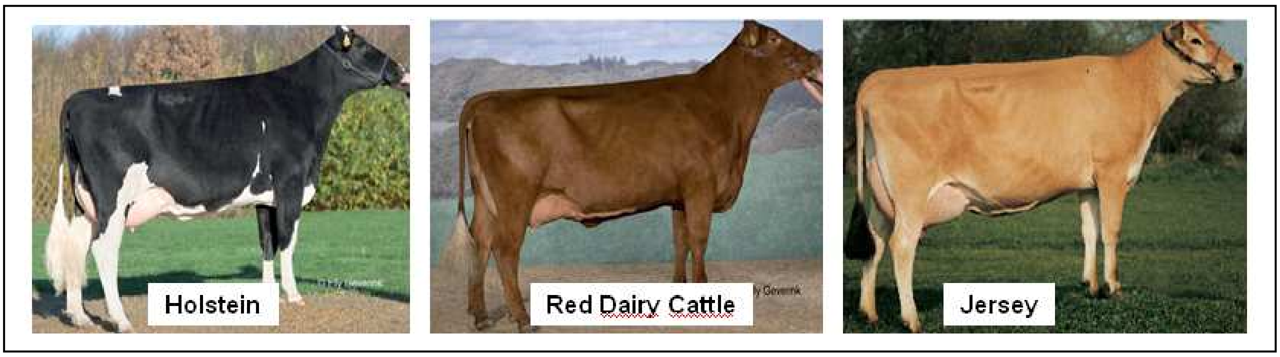

Figure 3. Beautiful representatives of the 3 main dairy cattle breeds in Denmark

Breeding Goal

The three Nordic countries, Denmark, Finland and Sweden, have joint breeding programmes and the same breeding goals, but the breeding goals differ slightly across the breeds. Breeding goals are decided upon by each breed association. However, to a large extent the associations base their decisions on results from analyses using bio-economic models of revenues and costs in a typical future herd. The Nordic Total Merit (NTM) index reflects the breeding goal of the particular breed (Table 1). The traits mentioned in Table 1 are in most cases sub-indexes made up of several individual traits, as described in the footnotes to the table. The value of a one-unit increase in the NTM index corresponds to 75, 58 and 67 DKK per cow per year for Holstein, Red Dairy Cattle and Jersey, respectively.

Feed efficiency is not assigned a direct economic value in the NTM indexes, because no registrations are available for feed efficiency. However, feed prices are taken into account in the bio-economic model, and they influence the economic values for dairy production. Hence, when feed relative to milk prices increases the economic values for functional traits relative to dairy production also increase. Such modelling is based on many critical assumptions. It could never be as sound as the kind of model that would be based on the inclusion of direct economic values if feed efficiency records were available on individual animals.

Table 1. NTM indexes for the 3 Nordic dairy breeds (NAV, 2008)

	Index weights[1]			Correlation(NTM, sub index)[2]		
	Holstein	RDC	Jersey	Holstein	RDC	Jersey
Dairy production[3]	0.75	0.92	0.87	0.42	0.56	0.72
Beef production[4]	0.06	0.00	0.00	0.01	-0.27	0.09
Female fertility[5]	0.31	0.26	0.26	0.46	0.23	0.25
Calf vitality[6]	0.15	0.14	0.06	0.33	0.38	0.21
Calving ease[7]	0.17	0.12	0.06	0.45	0.09	-0.19
Udder health[8]	0.35	0.32	0.49	0.48	0.53	0.47
Resistance to other diseases[9]	0.12	0.12	0.04	0.49	0.38	0.25
Feet and legs	0.15	0.09	0.05	0.17	0.19	0.16
Udder conformation	0.18	0.32	0.15	0.47	0.53	0.22
Milking ability	0.08	0.06	0.10	0.15	0.36	-0.05
Temperament	0.03	0.03	0.03	0.02	0.17	0.38
Longevity[10]	0.11	0.08	0.12	0.55	0.49	0.29

[1]b-values in selection index
[2]Indicates expected genetic progress (approximate as popular bulls have large influence and as it ignores that females lack EBV for some functional traits)
[3]Includes milk, fat and protein yield (most weight on protein)
[4]Includes growth and slaughter quality measured on the EUROP scale
[5]Includes days calving—first AI, days first—last AI, #AI and resistance to fertility disorders
[6]Whether or not calf is alive 24h after calving
[7]Calving ease scored by farmer using a scale from 1 to 4
[8]Mastitis resistance (binary trait) receives all direct economic weight, but correlated information from SCC and udder conformation
[9]Includes metabolic, feet & leg and reproductive diseases
[10]Risk of involuntary culling per lactation (economic value reflects what is not already explained by other traits such as udder health and fertility)

The breeding goals in the Nordic countries place a relatively strong emphasis on functional traits, and especially on health, due to high labour and veterinary costs. Non-Nordic countries keep no systematic records of health traits.

Genetic Evaluation and Parameters

Nordic Cattle Genetic Evaluation (Nordisk Avlsværdivurdering, NAV) computes EBVs jointly for Denmark, Finland and Sweden four times annually. Multiple-trait models are used for the traits belonging to the sub-indexes mentioned in Table 1. For instance, milk, fat and protein yield from 1st, 2nd and 3rd parity are treated as different traits using the estimated correlation structure among traits. Likewise mastitis in different parities and lactation stages is treated as a plurality of traits and analysed simultaneously with somatic cell-count, fore udder attachment and udder depth to increase the accuracy of predictions. Longevity, conformation and workability traits (milk ability and temperament) are analysed in single-trait models. Animal Models are used for dairy production, beef production, udder health, longevity, conformation and workability traits. Sire Models are used for the remaining traits. This means that EBVs for important functional traits are not available for females, except when they are based on paternal pedigree information. In the near future, genetic evaluations for claw health based on records from claw trimmers are expected.

The statistical models used for genetic evaluations include a number of different explanatory effects, such as herd, year, month and age associated with the given performance. These effects may be different for different traits depending on the frequency of measures, heritability, the selection emphasis, the biology of the traits and the evaluation method. For instance, daily yields are measured on different test-days, so the model for dairy production includes the effect of specific test-days rather than a monthly measure. The model for dairy production also accounts for the shape of the lactation curves, which makes it complicated. Further details of the evaluation models for specific traits can be found in the Danish Knowledge Centre for Agriculture (2010; in Danish) or Interbull (2010; for several countries).

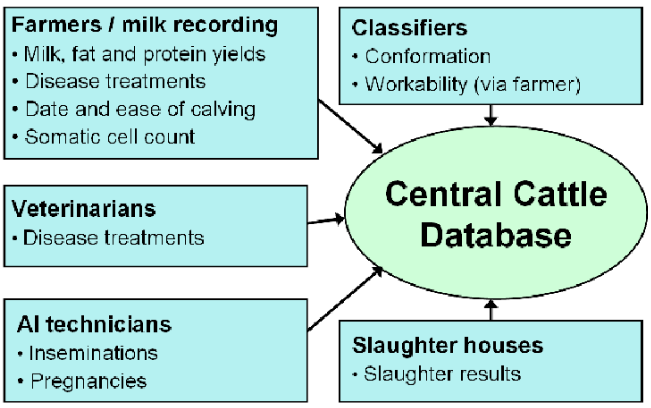

Figure 4. Sources of data used for genetic evaluation and other purposes. The quality and quantity of records are crucial for genetic evaluations.

Genetic parameters for different traits (or indexes) in the breeding programme are summarized in Table 2 for Holsteins. Heritabilities and correlations are similar in other breeds, whereas variances differ more. Generally dairy production has unfavourable genetic correlations with functional traits. The genetic correlations in Table 2 were approximated from EBV. A few of the estimates were more extreme (e.g. for dairy production with female fertility and other diseases, respectively) and others closer to zero (e.g. for longevity with female fertility and other diseases, respectively) compared with similar estimates in the literature.

Table 2. Approximate heritabilities (on diagonal) and genetic correlations (×10; above diagonal) for traits in the Holstein NTM index[1]

	A	B	C	D	E	F	G	H	I	J	K	L
A. Dairy production	**0.40**	1	-4	-1	-1	-3	-4	1	1	2	3	5
B. Beef production		**0.23**	1	0	0	-1	3	-3	-2	0	-1	1
C. Female fertility			**0.03**	2	3	3	5	-1	-3	-2	-2	0
D. Calf vitality				**0.03**	1	1	3	1	0	0	-1	1
E. Calving ease					**0.05**	1	4	1	-1	0	-2	1
F. Udder health						**0.03**	4	1	4	-2	-2	4
G. Other diseases							**0.02**	-1	-2	-2	-2	1
H. Feet and legs								**0.17**	4	1	1	2
I. Udder conformation									**0.29**	2	2	4
J. Milking ability										**0.26**	3	2
K. Temperament											**0.13**	2
L. Longevity												**0.10**

[1]In all traits a high index value is favourable, so all negative correlations are unfavourable. Heritabilities are weighted averages of those used for the genetic evaluation of individual traits, and genetic correlations were approximated from correlations among EBVs adjusted for reliability (in a few cases the approximated correlation was regressed towards previously available information such as relevant literature estimates).

International genetic evaluations for bulls are conducted three times annually by the organization Interbull so that objective comparisons of bulls across country borders can be made. All traits mentioned in Table 2 are evaluated, except beef production. A multiple-trait model is used within which performance in each country is considered a distinct trait, thereby allowing for country-specific selection according to own production circumstances. Across-country genetic correlations between milk yield in similar production environments such as Denmark and the Netherlands (0.92) are stronger than they are in less similar production environments such as Denmark and New Zealand (0.75), because cows in New Zealand are on pasture all year unlike those in Denmark and the Netherlands.

Genomic breeding values for genotyped animals have been calculated for all of the traits in the Nordic breeding goal since 2009. Other leading dairy countries have also implemented genomic predictions or are in the process of doing so. So far these calculations have been based on the traditional EBV, or functions of it, but a method integrating all of the information in one step is being developed. Practical results indicate that the reliability (r^2_{IA}) of genomic EBV ranges between 30–72% for all traits considered in the Nordic countries and between 41–53% for welfare traits; these figures are substantially higher than the average for parents' breeding values (Su *et al* 2009).

Organization and Breeding Programme

VikingGenetics is a farmer owned organization that is responsible for practical cattle breeding in Denmark, Finland and Sweden. Its responsibilities include selecting and testing bulls and producing and marketing semen, as well as conducting AI and advising farmers on breeding (e.g. on insemination plans).

Until recently dairy cattle breeding has not followed the breeding pyramid structure we see in pig and poultry breeding. This is mainly due to the low reproductive rate of females. Instead nearly all cows in the population are recorded and potentially available for breeding. Nor is crossbreeding widely used in Denmark (less than 10% of Danish dairy cows are crossbred), but it is widely used in New Zealand and is increasing in the USA. Widespread use of AI characterizes dairy cattle breeding, but the main traits are only expressed in females where the selection intensity is low because most of the heifer calves born are needed to maintain a constant population size. This has resulted in long generation intervals for sires, because intense bull selection was not optimal until progeny information was available. (Bulls were at least 5 years old when first daughters went into first lactation.) The breeding system used for decades in many countries, including Denmark, was a 4-pathway structure concerned with selection of sires for sires (SS), dams for sires (DS), sires for dams (SD) and dams for dams (DD).

In Danish Holstein, approximately 5–6 SS and 10–12 SD were selected per year from the 240 progeny-tested bulls. Similar proportions were also selected from 60 Swedish and 50 Finnish progeny-tested bulls. The selected bulls were 5–7 years old. At the same time about 2000 DS and 90% DD were selected from the cow population. The selected DS and DD are younger than SD and SS when they are selected, but before genomic EBV became available they had typically had at least one own lactation (i.e. were >2–3 years old). More SS than are needed are selected to avoid accelerated rates of inbreeding. Also, individual farmers avoid mating close relatives. To facilitate this VikingGenetics looks for bulls with alternative pedigrees in addition to EBVs when selecting SS and young bulls for testing.

Today the 4-pathway breeding system is being revised in responses to the recent availability of accurate genomic EBV at an early age. Countries have been quick to adopt this new technology, but little is still known about how it is best used to enhance genetic progress with low risk. Initially, then, more or less conservative modifications of the traditional 4-pathway structure are being implemented. In Nordic countries genomic EBV is presently used to intensify the pre-selection of young bulls to be progeny-tested and to identify bull dams (DS) for super-ovulation and embryo transfer. Thus, heifers with high genomic EBV are used as DS; young bulls with high genomic EBV are also being used to some extent. Although fewer young bulls may start progeny testing than before, the screening is expected to be much more accurate than the previous screening, which was based primarily on the average EBV of parents.

The following changes, which were made in the Nordic Holstein breeding plan after genomic EBV became available, illustrate recent developments (Lars Nielsen, VikingGenetics, pers. comm.):

- Young bulls (1.5–2.5 years old) with high genomic EBV (GenVikPlus) were used for 15% of all inseminations in August 2010
- About 1300 young bulls are genotyped and 225 of these initiate progeny testing
- Hence, about 33% fewer young bulls are progeny-tested than previously. In the future even fewer Holstein bulls are expected to be progeny-tested due to closer cooperation with other European Holstein populations (EuroGenomics). Other breeds do not have the same opportunities for cooperation, and therefore with these breeds it is not possible to reduce the number of progeny-tested bulls as much in order to maintain a sufficiently high accuracy of genomic EBV
- Up to 10 000 semen doses of each of the most promising young bulls, based on genomic EBV, are used immediately and approximately 10 000 semen doses are saved
- VikingGenetics genotype about 500 Holstein heifers and cows. In addition to this private farmers genotype some females
- About 20% of the waiting bulls (with initiated progeny testing, but awaiting progeny results) with the lowest genomic EBV are culled

In the future the availability of genomic EBV may lead to more fundamental changes in the breeding programme. For instance, although high quality data on a reasonable number of animals (the precise number depends on heritability, population structure, and so on: see the notes on genomic selection) are always crucial, data records for *all* animals are no longer required. Instead specific herds may be targeted for more intense data recording. Through the extended use of embryo transfer and sexed semen an open nucleus scheme with systematic crossbreeding in production herds can be envisaged.

Examples of Genetic Trends

Fig. 5 shows genetic trends for selected traits and the NTM for Danish Holstein bulls. In the 1990s most of the selection emphasis was on dairy production — at least, in reality, due to the heavy use of North American bulls. At the beginning of the new millennium the emphasis on functional traits such as udder health, longevity and female fertility increased. The onset of international genetic evaluations for these traits in 2001, 2004 and 2007, respectively, made it easier for the participating countries to select foreign bulls according to their breeding goals, especially for the Nordic countries which puts relatively strong emphasis on functional traits compared with other countries. By comparison, genetic trends for functional traits were not unfavourable for Red Dairy Breeds as they relied to a large extent on Nordic bulls.

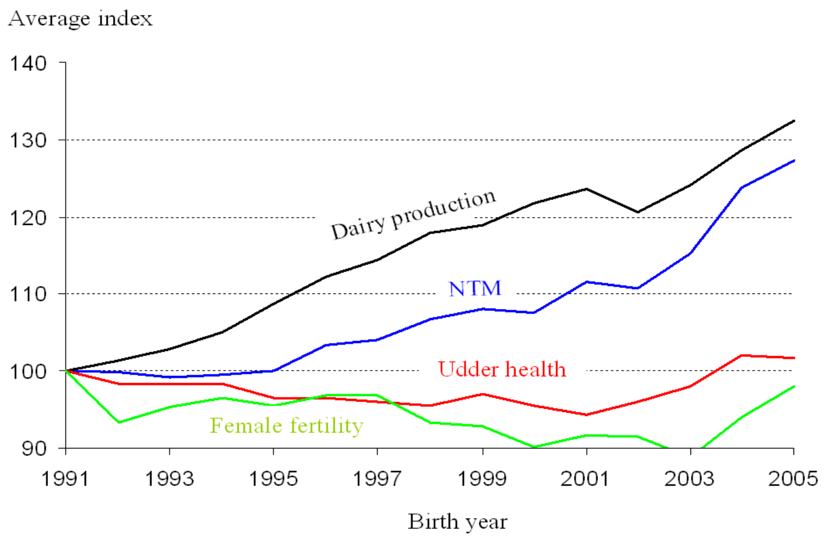

Figure 5. Development in average indexes of Danish Holstein bulls per birth year (Danish Knowledge Centre, 2010). Official indexes were standardized to equal 100 in 1991 to facilitate comparisons. NTM is the Nordic total-merit index described in Table 1.

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Poultry Breeding

Birgitte Ask

Introduction

Industrial poultry breeding involves a wide range of species (chickens, turkeys, ducks, geese, quail, and ostriches) and purposes (eggs, meat, feathers, leather, and oil). Both in Denmark and worldwide it is chickens — for eggs (layers) and meat (broilers) — that are most numerous and economically important bird in industrial poultry breeding. Worldwide, turkey and duck breeding also operate on quite a large scale and are important, whereas geese, quail, and ostrich breeding can generally be categorized as small-scale industrial breeding for niche production. In Table 1, the production size and number of herds in Denmark and the worldwide production size are given for various industrial poultry breeding species.

Table 1. Production size and herds in Denmark and worldwide for various industrial poultry species (2010 figures).

	Denmark		Worldwide	Main Production
Species: main product	Production size	N herds	Production size[1]	Countries
Chickens (Layers): eggs	67 mio kg	3096	>60.7	CN, USA, IN, JP
Chickens (Broilers): meat	198 mio kg	286	>79.4	USA, CN, BR, MX
Turkeys: meat	12 mio kg	85	>6.1	USA, FR, DE, IT
Ducks: meat	1.6 mio birds	265	>3.8	CN, FR, TH, TW
Geese: meat	14 000 birds	215	>2.4	CN, UA, HU, EG
Guinea fowl/quail/other: meat	Unknown	Unknown	>218	CN, ES, FR
Ostrich/emu: leather and meat	2000 birds	50	>535 000 birds	ZA, CN, BR, AU

[1]Given in million tonnes unless otherwise stated

The reproductive capacity of poultry is generally high. This is especially so with chickens, which have a particularly high female reproductive capacity compared with other species. This gives poultry some of the shortest generation intervals in farm animal breeding (see Table 2). Another important feature of poultry breeding is that males are homogametic (ZZ), whereas the females are heterogametic (ZW). This affects which reproductive technologies are possible and also crossbreeding organization.

Table 2. Male and female reproductive capacity (number of females per male; eggs per hen per year / hatchability) and the generation interval of various industrial poultry breeding species.

	Pure Lines		Product (crossbred)	Generation
	Male	Female	Female	Interval
Chickens (Layers)	8–15	Unknown	260–305 / >90%	1–1.5 yrs
Chickens (Broilers)	6–14	50–110 / 50–90%	180 / 75–90%	8–12 mth
Turkeys	6–14	Unknown	100–120 / 75–90%	1–1.5 yrs
Ducks, Pekin &	6–10	225 / 85%	225 / 60%	1–1.5 yrs
Muscovy	5	85 / 80%		
Geese	9	30–70 / 70%	Unknown	1–1.5 yrs
Quail	4–8	290 / 50–76%	Not applicable	~18 wks
Ostrich	2	25–100 / >50%	Not applicable	6–8.4 yrs

Breeds

For a number of species the most important breeds used in industrial poultry breeding are given in Table 3. It is worth noting, however, that in most major poultry breeding operations the term *breed* is now rarely used. Rather, the terms (pure or pedigree) *line* and (final) *product* are used.

Lines originate from one or more breeds; they are bred and selected in closed populations. A distinction is made between so-called sire and dam lines — which, in species kept for meat production, usually originate from different breeds.

Products are the birds that are used in the final market operation. In layers, for instance, they are the birds that produce eggs for consumption, and in species kept for meat production they are the birds that are produced for meat consumption. Products are usually line crosses, in some cases between lines originating from different breeds.

Table 3. Breeds used in various industrial poultry breeding species.

Species mainly for egg production	White eggs	Brown eggs	
Chickens (Layers)	Leghorn	New Hampshire, Rhode Island Red, Barred Plymouth Rock, Australorp	
Species mainly for meat production	**Sire/Heavy Breeds**	**Dam/Lighter Breeds**	**Alternative Use Breeds**
Chickens (Broilers)	White Cornish	White Plymouth Rock	Cou Nu (ecological production), 'Chinese Yellow Chicken' (many breeds)
Turkeys	Broad Breasted Bronze, Broad Breasted White		
Ducks	Muscovy (Berberie)	Pekin	Foie gras production: Moulard
Geese	Embden	Toulouse, Italian	
Quail	American	Japanese	

Breeding goal

A detailed listing of traits included in the breeding goals of various industrial poultry breeding species is given in Table 4. Comprehensive studies of the economic and social values in poultry breeding programmes have not been published, except for economic values in broilers. Examples for some traits are provided in Table 4, but values will depend on the market (e.g. battery or floor-housing egg production, and live bird or processed meat production). Many poultry breeding companies are applying a desired gains approach rather than using economic values based on cumulative discounted expressions.

The general breeding goal for laying hens includes traits related to: high number of saleable eggs per hen, feed conversion, egg quality, mortality, and adaptability to specific commercial environments. Interest in adaptability increasingly focuses on floor management and involves traits such as nesting behaviour, feather pecking, and cannibalism.

Table 4. The most important traits in the breeding goals for various industrial poultry species (conventional markets) and some examples of economic values (only current for ostriches).

Trait Group	Layers	Broilers (Turkeys, Ducks, Geese)	Ostriches
Egg / Meat production	Age 1st egg, hen-day egg production, persistency of production (0.6029/%), broodiness, egg size/weight (-0.8111/gram)	Growth, body weight at slaughter age (0.7297 Dfl/kg), carcass- (0.0735 Dfl/%), breast meat- (0.1373 Dfl/%), and other body part yields	Growth (11.0 ZAR/slaughter bird) /Body weight, skin size
Production efficiency	Mature body weight, feed conversion (1.6733/0.1 unit)	Feed conversion, abdominal fat	Feed conversion
Reproductive performance	Female and male fertility, hatchability	Age 1st egg, hen-day hatching egg production (0.0030 Dfl/no.), egg weight, female and male fertility, hatchability (0.0060 Dfl/%)	No. of eggs and quality day-old chicks (22.1 ZAR/slaughter bird), egg weight, hatchability
Product quality	Egg deformation, shell strength, thickness, and porosity, fishy odour, albumen and yolk weight	Drip loss, pH, meat colour	Nodule size and shape, neckline length, skin damage
Functional traits	Heat tolerance, disease resistance, leg strength, survival, cannibalism, flightiness	Egg deformation, survival/mortality (-0.0205 Dfl/%), leg health (e.g. tibial dyschondroplasia, femur head necrosis), ascites, infectious diseases	Survival
Others	Plumage and egg (shell) colour	Plumage and skin colour	No. of quill and short feathers

For broilers the main breeding goal is, and has always been, body weight at slaughter age. Many other traits are also included in the breeding goal, though. For example, feed conversion, slaughter yield, mortality, leg health and cardio-respiratory health, and female and male reproduction traits. In recent years, quality traits have also been included for some markets. These include one or several of the following: body conformation, intramuscular fat, tenderness, drip loss, plumage-, skin-, and shank colour, comb redness and size, and feathering rate.

The breeding goals for turkey, duck and geese are generally similar to those for broilers. They exclude cardio-respiratory health, however, as this problem chiefly affects the very intensively selected broilers.

The main driver in duck breeding has been consumer demand for lower-cost food products. The principal foci of the breeding goal were initially (1970s to early 1980s) body weight, laying performance and survival ability; but afterwards (until 2000) the focus became broader, as changes in housing systems and breeding industry expansion occurred. The breeding goal now came to include traits such as feed conversion ratio, body composition (high meat and low fat yield), leg strength, fertility, hatchability, egg weight and eggshell quality. Since 2000 even more traits have been included in the breeding goal, including sexual behaviour traits (fertility) and mobility (leg strength), but disease resistance and health disorders have only very recently (2006 on) come under consideration. Specialized breeding companies focusing on foie gras production have a slightly different focus (not low fat yield, but high liver yield). If economic values are used, none have been published. It is possible that a desired gains approach is used rather than economic values.

In ostrich breeding, the economically most important traits serve leather and meat production, and to some extent feather quality. In recent years, there has been a shift towards meat production. The relative importance (b-values) of leather, meat, and feathers was approximately 70%, 25%, and 5%, respectively, about a decade ago; today the corresponding figures are 45%, 45%, and 10%.

The distinction between the sire and dam lines mentioned earlier is reflected in breeding goals. The sire line is a line bred with the purpose of obtaining an outcome in the male at the parent stock level in the breeding pyramid, whereas the dam line is bred with the purpose of obtaining an outcome in the female at parent stock level (see below, Organization and Breeding Programme). This differentiation in of the breeding goals involved in sire and dam lines should ensure that there is positive heterosis in the final product (Fig. 1A).

In the breeding goal of layer sire lines relatively large weight is placed on egg quality and male reproduction traits. In the breeding goal of broiler sire lines, by contrast, more weight is attached to production traits such as body weight and breast meat yield, as well as to male reproduction traits. In both layer and broiler sire lines relatively little weight is placed on female reproduction traits.

In the breeding goal of layer dam lines the main focus is on female reproduction traits. In the breeding goal of broiler dam lines relatively little weight is placed on production traits such as body weight and breast meat yield and more weight is placed on female reproduction traits.

Genetic Evaluation and Parameters

In the larger poultry breeding companies targeting conventional markets, genetic evaluations are mainly conducted using BLUP animal models, although phenotypic culling is also applied sometimes, especially for functional traits. In some companies, multi-trait models are used to the extent allowed by computer processing limitations, but some companies still apply single-trait models. Advanced models, including non-additive genetic effects (e.g. common environment, maternal or heterosis effects) are used by some companies, and the inclusion of genetic markers is gradually being implemented by various companies. Smaller (and often local) breeding companies apply mostly mass selection based solely on phenotypic information.

Table 5. Heritabilities (on diagonal), genetic correlations (below diagonal) and phenotypic correlations (above diagonal) of some important breeding goal traits in layers.

Trait[1]	AFE	BW	EP	EW	ESS	ESC	AH	YW	Surv
AFE	0.32	0.03	-0.21	0.05	-	-	-	-	-
BW	0.10	0.45	0.11	0.09	-	-	-	-	-
EP	-0.34	0.28	0.18	-0.02	-	-	-	-	-
EW	0.27	0.09	-0.28	0.63	-0.05	-0.08	0.22	0.71	-
ESS	-	-	-	-0.19	0.24	-0.20	-0.02	0.00	-
ESC	-	-	-	-0.12	-0.13	0.46	0.00	-0.13	-
AH	-	-	-	0.32	-0.25	-0.02	0.51	-0.03	-
YW	-	-	-	0.77	0.08	-0.21	0.07	0.45	-
Surv	-	-	-	-	-	-	-	-	0.02-0.10

[1]: AFE: age at 1st egg; BW: body weight at 40 weeks; EP: egg production (%) at 64 weeks; EW: egg weight at 28 weeks; ESS: eggshell strength; ESC: eggshell colour; AH: albumen height; YW: yolk weight; Surv: Survival days.

Examples of typical genetic parameters for important traits in layers and broilers are given in Table 5 and Table 6, respectively. The number of studies reporting genetic parameters for important traits in turkey, duck, geese, and ostrich breeding is limited, but the studies published so far report heritabilities that are generally in the same range as those reported for broilers — except for heritabilities of body weight in geese, which were very high (e.g. 0.50±0.05 to 0.64±0.05).

Table 6. Heritabilities (on diagonal) and genetic correlations (below diagonal) of important breeding goal traits in broilers.

Trait[1]	BW	FCR	RV:TV	BMY	AFY	CC	pH	TD	SDS	FPD
BW	0.24	-	-	0.18	0.12	-	-	-	-	-0.02
FCR	0.35	0.16	-	-	-	-	-	-	-	-
RV:TV	-	-	0.28	-	-	-	-	-	-	-
BMY	0.12	-	-	0.73	-0.39	-	-	-	-	-
AFY	0.13	-	-	-0.28	0.71	-	-	-	-	-
CC	-	-	-	-	-	0.09	-	-	-	-
pH	0.08	-	-	-0.12	-0.76	-	0.49	-	-	-
TD	-	-	-	-	-	-	-	0.4-0.65	-	-
SDS	0.30	-	-	-	-	-	-	-	0.35-0.45	-
FPD	-0.51	-	-	-	-	-	-	-	-	0.08-0.21

[1]: BW: body weight at 42 days; FCR: feed conversion ratio; RV:TV: ratio of right ventricle to total ventricle weight; BMY: breast meat yield; AFY: abdominal fat yield; CC: cecal carriage of salmonella; pH: pH of breast meat; TD: tibial dyschondroplasia incidence; SDS: sudden death syndrome; FPD: footpad dermatitis severity.

For genetic evaluations in the pure lines of large companies (breeding layers, broilers, turkeys and, to some extent, ducks) single-trait and/or multi-trait BLUP are used, but selections based on BLUP-EBV are usually accompanied by more or less elaborate phenotypic culling. Great grandparent stock may also be selected on the basis of genetic evaluations, but it is only in the grandparent and parent stock that phenotypic culling is applied. The inclusion, by poultry breeding companies, of genomic information in genetic evaluations is becoming more and more common. It enables selection to be based to some extent on genome-wide breeding values. More companies are expected to join this trend. Molecular genetic information has already been used successfully for simple inherited traits in some poultry breeding programmes. For example, genetic tests are used to identify the presence or absence of specific colour genes in connection with the development of coloured broiler lines for alternative production systems. In layers, an example of a successful genetic test is the test for fishy taint in eggs (the *FMO3* gene). This test has allowed the taint problem to be eliminated in most, if not all, commercial lines today. In smaller scale breeding companies (especially those working with geese, quail and ostriches) classical selection index or even pure mass selection is still practised.

Organization and Breeding Programme

Today layer, broiler, turkey and duck markets deal mainly in the final products (Fig. 1A) of just a few large-scale, centralized breeding companies. For decades the companies have been specializing in, and merging within, each species, and therefore growing. During the past few years, however, there has been a trend for specialized companies to merge into multi-species companies, with a range of products for each species. The major companies include the *Erich Wesjohann Gruppe*, which concentrates on products in the white and brown layer (*Lohmann Tierzucht, Hyline, H&N*) broiler (*Aviagen*) and turkey (*Aviagen, British United Turkeys*) markets; *Hendrix Genetics*, which concentrates on products in the white and brown layer (*ISA, Hendrix*) and turkey (*Hybrid*) markets; the *Grimaud Group*, which concentrates on products in the broiler (*Hubbard*) and duck (*Grimaud*) markets; and *Tyson* (broilers: *Cobb-Vantress*) and *Bangkok Ranch Group* (ducks: *Bangkok Ranch, Cherry Valley*). The major driver of the formation of these multi-species companies has been collaboration in research projects, particularly in genomics. In Asia and Africa, especially, large parts of the poultry markets are, however, still concerned with local breeds that have been bred in small companies or small-scale holdings — for example, the Yellow Bird, which is a local Chinese meat-bird product.

The typical breeding pyramid structure of the poultry breeding industry is shown in Fig. 1B. The pure-line elite stock is located at one main location, preferably minimized to one satellite farm. A satellite farm is essentially a backup breeding programme, which is a copy of the central one, but which is located elsewhere to spread any risks presented by, for example, A-list diseases. At the pure-line level, a breeding company typically has a number of commercial as well as experimental lines. The commercial lines are used in final products currently being marketed; experimental lines are developed for potential new products of the future, or for the exchange of lines in current products. A final product is typically a three-way or four-way cross, as shown for broilers in Fig. 1A. The breeding programme is at the pure-line elite stock level, possibly with simultaneous measurements at great grandparent stock level (which can be used as additional information in the genetic evaluations). The great grandparent, as well as the grandparent, stock levels are, however, primarily multiplier levels. The parent stock level, like the final product level itself, is considered a production level. There are four generations (4–5 years) between the pure-line and final product level. Thus there is always a genetic gap between pure lines and production birds at the final product level.

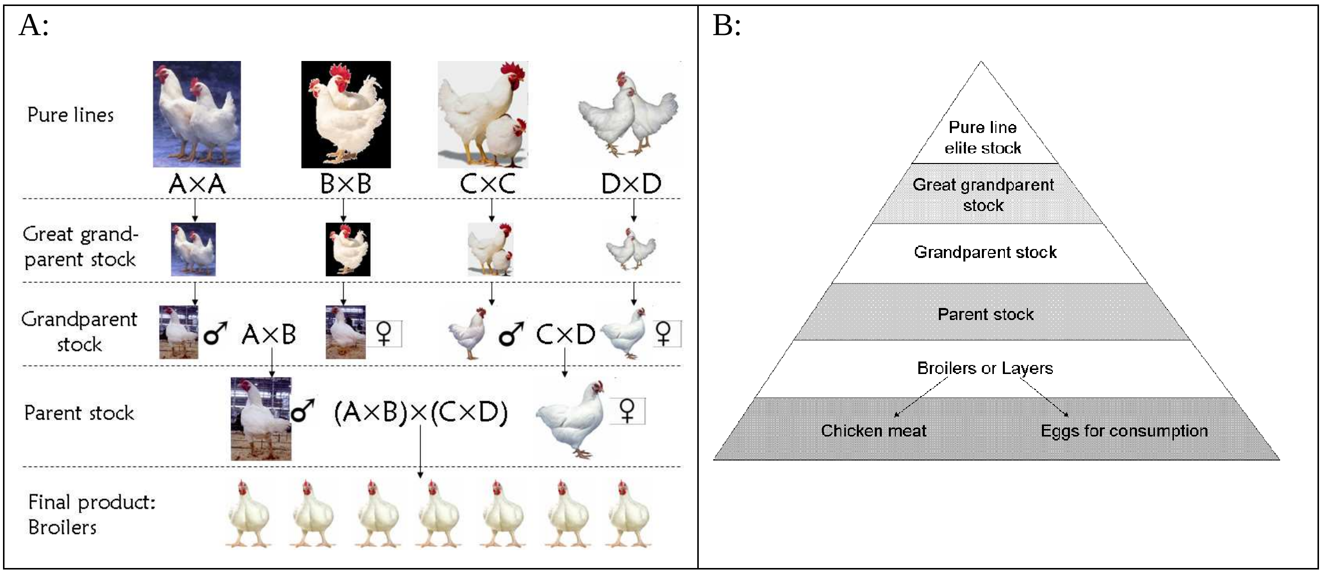

Figure 1. A: The crossbreeding system in the breeding pyramid exemplified by broilers, where A and B are sire lines and C and D are dam lines; B: The breeding pyramid structure of the poultry breeding industry exemplified by broilers or layers and showing the flow of birds from pure-line elite stock.

Currently the potential of lines as either sire or dam lines is limited by the feather sexing procedure used to distinguish 1-day old male and female chicks at final product level (this distinction allows the separation of males and females for a quicker turnover). Feather sexing makes use of a genetically determined differentiation in feather growth. The dominant sex-linked gene, K, results in slow feathering; the recessive allele, k+, results in fast feathering. In slow-feathering chicks the primary wing feathers are short and no longer than the coverts. By contrast, primary wing feathers are longer than the coverts in fast-feathering chicks. In the final product males must be slow-feathering and females fast-feathering, and to achieve this, the sire lines must be fast-feathering and the dam lines used as a male at grandparent stock level (C) must be slow-feathering; dam lines used as a female at grandparent stock level can be either fast or slow.

A multi-stage selection strategy, with at least two selection steps, and an overlapping generation structure is usually adopted in poultry breeding. Typical breeding programmes in layers and broilers are illustrated in Fig. 2. To a great extent, these are representative of other meat production species as well.

In layers performance tests of pure lines and crosses (by reciprocal recurrent selection) for feed efficiency (production/feed intake) and reproduction traits, among other traits, are run roughly between 20–50 weeks of age. Reciprocal recurrent (i.e. repeated in each generation) selection is based on the performance of cross-line relatives by assigning sires of each line to be mated to dams of each line and the other way around. The crossbred offspring can then also be performance-tested. There is one pre-selection step (1st step: during rearing) and one or two selection steps during the production period (e.g. 2nd step: after peak production and 3rd step: well through the production period — between 50 and 60 weeks of age — in order to include information on persistency and information from the reciprocal recurrent testing). Matings may be reshuffled after the 3rd selection step. Selection intensities are high, and an approximation of the selected proportions within a generation is that ~0.2–0.5% of males and ~1–3% of females are kept for reproduction of the next generation.

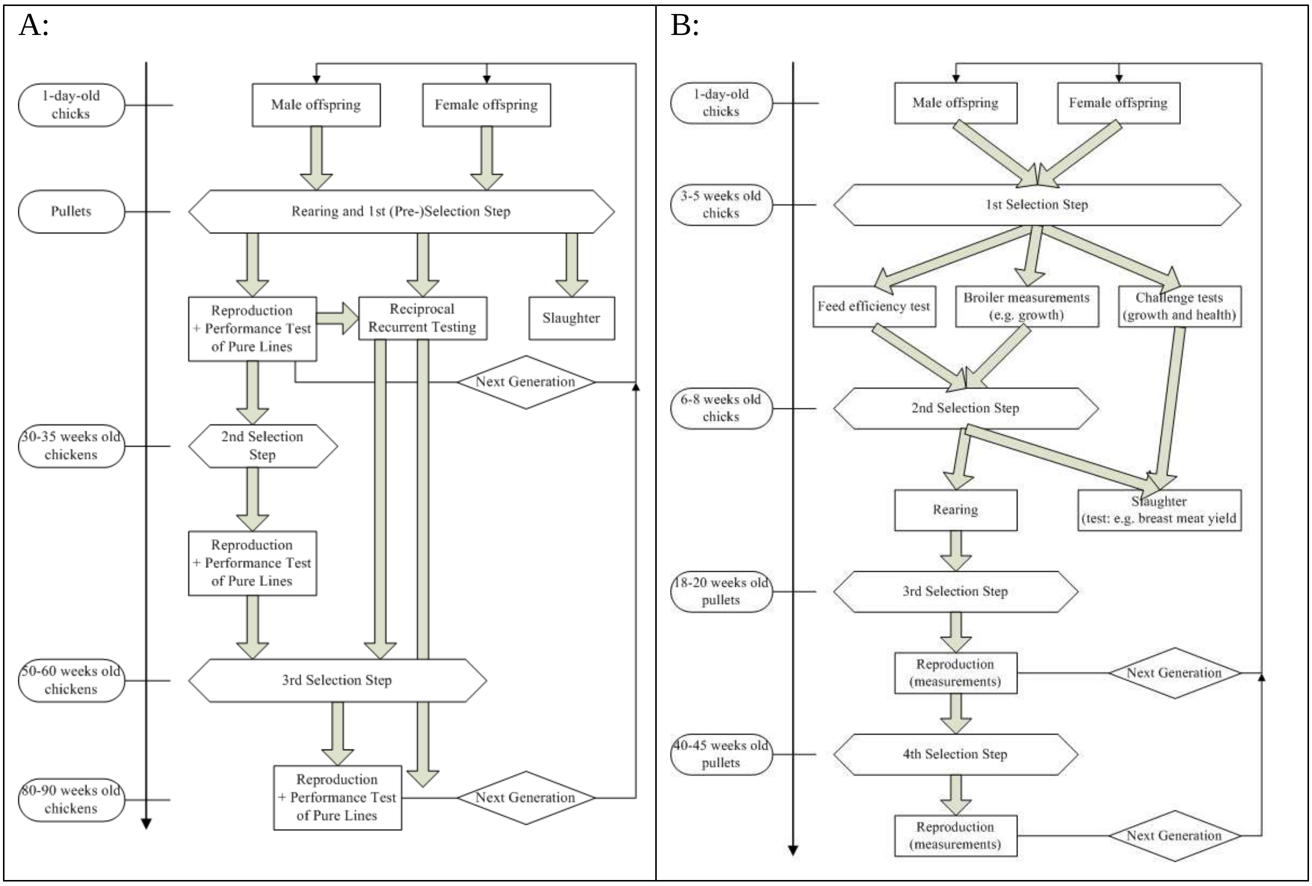

Figure 2. A: A typical breeding programme for pure-line layers; B: A typical breeding programme for pure-line broilers. 'Tests' refers to situations where a transfer from one housing system or placing is required, whereas 'measurements' refers to situations where in principle no additional transfer is required for the gathering of information.

In broilers performance tests are conducted between approximately 3 and 8 weeks of age. They include feed efficiency testing in individual cages, slaughter tests for, among other things, meat yield, and health and performance testing in challenging environments. Testing focuses mainly on the pure lines and only to a limited extent on crossbred offspring. There are one or two selection steps at an early age (in broilers: 1^{st}: 3–5 weeks of age; 2^{nd}: 6–8 weeks of age), where the first (if present) corresponds to a transfer of (a part of) the birds to specialized test facilities, and the second corresponds to the age at which that species would normally be slaughtered as a final product. In addition, there are one or two selection steps for older birds: one prior to the egg-laying period (3^{rd} step) and one (some time) after peak egg production (4^{th} step), where, after matings, birds may be reshuffled. The 1^{st} and 4^{th} selection step are often differentially applied to males and females and are sometimes applied only to males. Selection intensities are higher in the first two selection steps than they are in the last two selection steps. An approximation of the selected proportions within a generation is that ~0.5–1% of males and ~2–4% of females are kept for reproduction of the next generation, depending on, among other things, the reproductive ability of the line (a higher selection intensity is possible in dam lines).

The only reproduction technology employed is AI, but it is widely used. Poultry semen cannot be stored for long, as freezing techniques are not well-developed; nor can it be diluted much. Generally, the number of females per male is therefore no higher when AI is used than it is in natural mating. The main advantage of AI relates to the control, and knowledge, of the full pedigree, and the fact that there is often a higher fertilization percentage in AI than there is in natural mating. The sexing of eggs (or embryos) before, or during, incubation is not currently feasible. A new method of sexing young embryos, which involves determining the dosage of the Z-linked gene DMRT1 in young embryos, is currently being developed for industrial purposes.

Inbreeding is a high risk in poultry breeding, given the high selection intensities applied, and in layers slight inbreeding depressions in sexual maturity and fertility have been reported. Until recently, the avoidance of full- and half-sib matings and the selection of a maximum number of offspring per sire has been the typical strategy deployed to manage inbreeding. In recent years, however, optimal genetic contributions theory is being implemented by larger companies. The poultry breeding industry is perfectly organized for this, as all matings are usually within company control (at least to the extent that AI is used).

Examples of Genetic Trends

In layers a genetic increase in the number of eggs produced of about 1.8 eggs per year was achieved in the period 1950–1993. In the same period, egg mass improved by ~43%, egg weight by ~12%, and feed efficiency by ~32%.

Historically, broilers have been one of the best examples of just how effective traditional quantitative breeding methods can be in obtaining genetic gain. Growth rate in them saw a fivefold increase over the period 1950–2000, with genetic gains in body weight of 58 g per year from 1957 to 1976, 73 g per year from 1976 to 1991, and 84 g per year from 1991 to 2001. In 2010 continued yearly genetic gain of ~50 g body weight at ~6 weeks of age is not unusual (actual genetic gain depends on how much weight is put on other traits in the breeding goal). In the period 1950–1993 carcass yield was improved by 91% and feed conversion by 63%.

In Fig. 3 genetic gains in some broiler, duck and goose traits are shown. In contrast with the gains observed for layers, broilers and ducks (shown in Figs. 3A, 3B, and 3C), no genetic gains have been observed in geese (Fig. 3D); this is probably due in part to the use of sub-optimal methods for genetic evaluations.

The genetic gains in desired traits are accompanied by correlated developments in other traits that are sometimes undesired. For example, in broilers, turkeys and, to some extent, ducks many health-related traits have been negatively affected by commercial selection pressure. These traits relate to the circulatory system (sudden death syndrome and ascites) and the musculoskeletal system (tibial dyschondroplasia, femur head necrosis, deep pectoral myopathy). In layers the worsening of traits such as flightiness, cannibalism and feather pecking, anorexia, and unenthusiastic nesting behaviour are also believed to be connected with commercial selection. Most poultry breeding programmes are now trying to minimize such consequences — for example, by recognizing the problematic traits in breeding goals and setting up tests to gather phenotypic information on them.

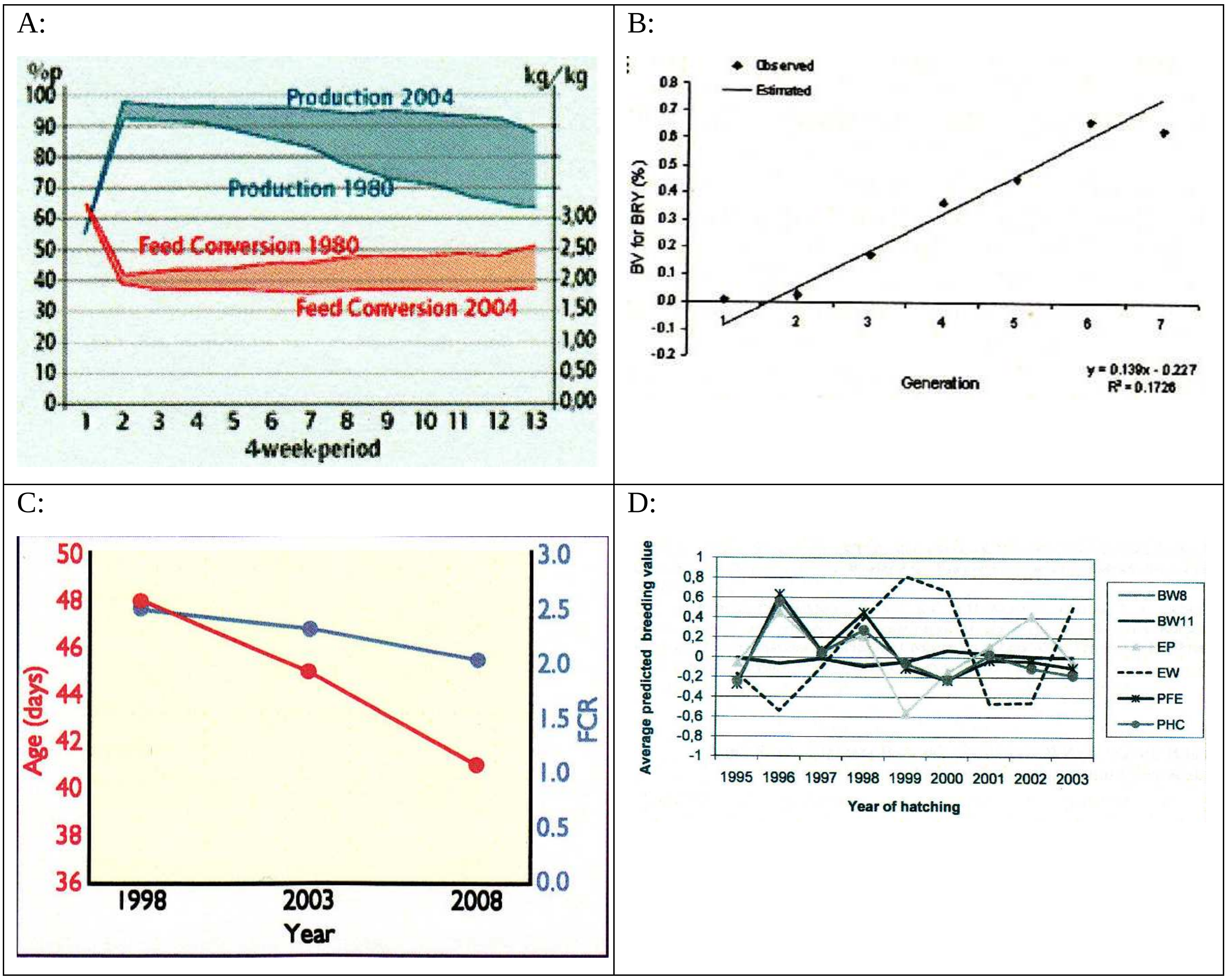

Figure 3. A: Difference in genetic level of egg production and feed conversion in layers 1980–2004 (Flock, 2009). B: Genetic trend of breast meat yield (breast meat / body weight) in a commercial broiler line (Grosso et al., 2009); C: Genetic improvement in slaughter age and feed conversion ratio (FCR) in Pekin ducks at a fixed weight of 3.3 kg (Grimaud, 2008). D: Genetic trends in a goose sire line of body weight at 8 and 11 weeks (BW8 and BW11), egg production (EP), egg weight (EW), percentage of eggs fertilized (PFE), and percentage of eggs hatched (PHC) (Wolc et al., 2008).

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Recommended books, homepages etc:

Books: Muir, W.M.; S.E. Aggrey. 2003. Poultry genetics, breeding, and biotechnology. Pp.720. CABI International. ISBN: 0-85199-660-4.

News and articles:	Http://www.thepoultrysite.com
	Http://www.wpsa.com
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	Http://www.grimaud.com/en/mission_index.html
	Http://www.cobb-vantress.com

Fur Animal Breeding

Thomas Mark, Knud Christensen & Peer Berg

Introduction

The main purpose of fur animal production is the production of fur for the textile and fashion industry. Most fur (85%) comes from farmed fur animals, but fur from wild animals (e.g. hunted by indigenous people) is also traded. The most commonly farmed fur animal in Denmark and worldwide is the mink (*Neovison vison*), followed by the fox (including the blue *Alopex lagopus* and the red sort *Vulpes vulpes*). Other species, farmed on a smaller scale, include nutria (e.g. *Myocastor coypus*), chinchilla (*Chinchilla lanigera*), fitch (*Mustela putorius* and *Mustela eversmanni*), sable (*Martes zibellina*) and Finn raccoon (*Nyctereutes procyonoides*). Most fur (both farmed and wild) is sold via international auction houses.

Denmark is the world's largest producer of mink fur. This is mainly due to convenient feed supply from animal by-products (e.g. from the fishing and slaughter industry), the availability of cheap straw, infrastructure required by, for example, feed production, a favourable climate, and tradition. In Denmark the number of breeding mink females has been broadly constant over the past 25 years (and was at 2.7 million in 2009). On the other hand, the number of mink farms decreased from more than 5000 in the late 1980s to about 1400 in 2009 (Clausen, 2010), so the average herd size has grown (and was just below 2000 breeding females in 2009).

Figure 1. Examples of fur use in the fashion industry

The graph in Fig. 2 shows numbers of pelts sold at the Danish fur auction and the corresponding worldwide sales between 1960 and 2010. The latter — global sales — follow the average price per pelt quite well. Other fur producing countries include China, Russia, Ukraine, Canada, the USA, the Netherlands, Finland, Norway, Sweden, South Korea, Poland and Argentina. Major exporting countries such as Denmark have a fur auction (e.g. Kopenhagen Fur). The vast majority of fur sold at Kopenhagen Fur is produced in Denmark, but pelts from other countries such as Sweden are also sold there. Likewise, a few (<5%) Danish produced pelts are sold abroad. China has a large home market and therefore exports relatively few pelts. It therefore does not figure in the data on world production.

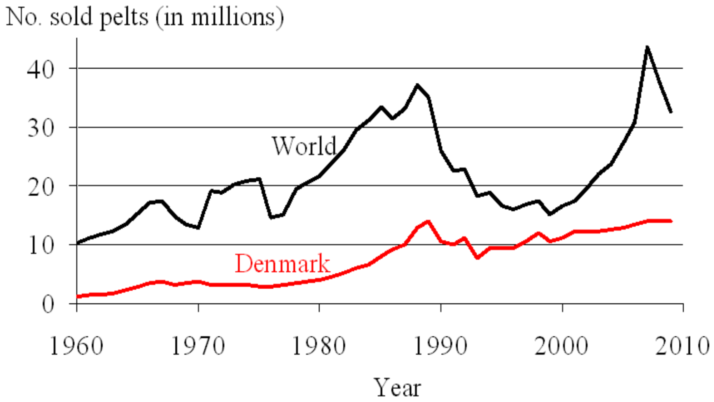


Figure 2. Number of pelts sold at auction in Denmark and worldwide (Source: Kopenhagen Fur).

Mink are housed in cages holding 1–4 animals. Typically, one male and one female pup are put in a cage together to avoid fights. After pelting, when there is more space available, there is only one female per cage. The minimum size of the cage is regulated by legislation to ensure a certain standard of animal welfare. In Denmark, farmed fur animals must also have access to straw and either a shelf or cylinder. Despite of these environmental enrichments, ethical concerns remain an issue among animal rights organizations over suppressed natural behaviour and injuries from the bites of cage-mates. Fig. 3 illustrates typical Danish mink environments. The main fur animals are carnivores, and their feed contains animal bi-products. Rodent species such as chinchilla, beaver and rabbit are used very little.

Figure 3. Two examples of Danish mink farms

Mink production follows a fixed seasonal cycle that depends on the reproductive cycle and fur development of the animals (stimulated by changes in the amount of daylight). In Denmark minks are naturally mated in March. The female is in heat for about 3 weeks and each male can only mate with 5–6 females per season. Mating induces ovulation, and the aim is to mate females twice per season. This results in a period of gestation that varies in length from 42 to 72 days, but is generally longer for early matings. Accordingly, most kits are born within 2 weeks around the 1st of May. Mean litter size is approximately 5.5 weaned kits per female (weaning occurs at ~8 weeks).

Breeds

Breeds are usually defined according to fur colour, and indeed the term 'colour type' is often used instead of 'breed'. However, within each colour type there can be several strains with different characteristics. The wild mink is brown, but animals with colours ranging from white to black are a result of mutations in colour genes. The black type, however, is special, as the degree of darkness is a polygenetic trait and the black colour type is therefore a result of several generations of selection. With the exception of black, fur colour type is a qualitative trait based on mutations. At least 25 different loci affect fur colour (Nes et al., 1998; Lohi et al., 2001), many of them with a number of different alleles (mutations). Although the fur colour type is a qualitative trait, there is polygenetic variation within colour type with respect to darkness and colour clarity. In the Nordic countries the development of mink mutations was at its height in the 1960s and 1970s — for foxes it was the 1980s (Lohi, 1993). The production of colour types varies somewhat from year to year, according to fashion trends. When prices for a specific colour type increase the breeders tend to react by preparing more animals with this colour type. Average litter size differs between colour types (Østergaard, 2010), ranging from 5.9 (brown) to 4.5 (violet). Of the more frequent colour types, black is known to have relatively small litter size (5.0). This could be due to the fact that inbreeding is more serious for the black type because it cannot be outbreed with other colour types without hampering the black colour that is a result of several generations of pure breeding. Another possible explanation refers to the pleiotropic effects of alleles for dark colour. The other colour types can more easily be used mutually as the original colour type is easily restored after one generation of backcrossing. Mahogany is a ‘synthetic breed’ originally created by crossing black and brown animals.

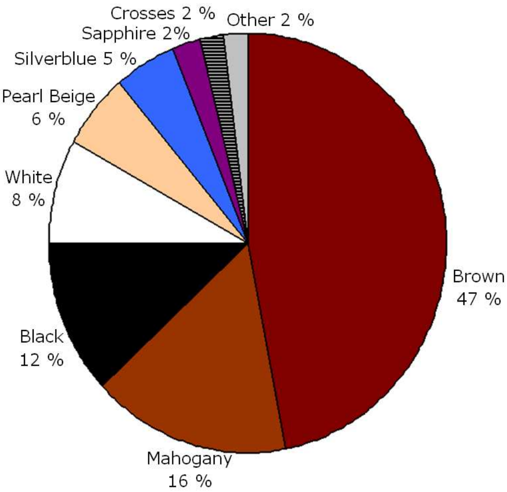
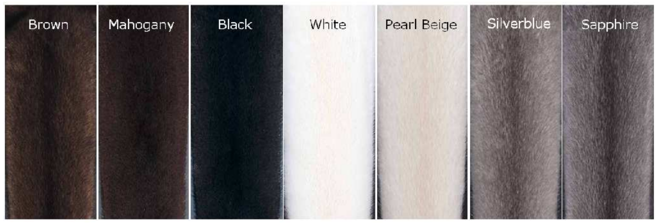


Figure 4. Distribution of mink colour types (or ‘breeds’) in Denmark (Clausen, 2010)



Breeding Goals

Breeding goals are farm-specific. Each breeder decides which traits should be included in selection decisions and what weight should be put on each trait. In practice many breeders use software based on a desired gain approach. They look at the expected realized genetic gains that will be achieved for each trait given the relative weighting factors and the estimated breeding values of animals at the farm. Given the fur colour type, typical traits included in selection decisions are overall fur quality (e.g. hair density, fur purity, hair length, hair elasticity, colour shade and colour darkness), pelt size (selected through body weight, as this and pelt size are strongly correlated) and reproduction (e.g. litter size). Furthermore, several traits such as health, and temperament (e.g. degree of stereotypic behaviour, pelt gnaw) are considered for pre-selection based on a subjective overall phenotypic assessment (which is used because most farmers do not systematically record these traits). All traits in the farm-specific breeding goals are recorded by the farmer and most of them are subjectively scored. For instance, fur quality is scored in November at the same time as weighting and before pelting. Not all animals have their fur quality scored, as this would be too time-consuming. Feed efficiency is currently not considered and this may cause the value of pelt size to be overestimated. There is some interest in breeding animals that utilize their food better, especially on farms that already register the amount of feed given to each animal. However, this would require an additional weighing of the animals after they have been weaned (e.g. in August). The weight gained relative to the amount of feed provided is a result of both feed utilization and behaviour, since the latter affects feed waste.

Most often, November weight and litter size are included in the breeding goal, receiving approximately the same relative weights. Fur quality is also very important, but the focus on this trait varies more between farms and depends on the farmer's ability and interest in scoring the fur characteristics of his animals. If, on a particular farm, the farmer considers one of the traits especially problematic (e.g. too low litter size), the relative weight of this trait will typically be increased. Farmers typically do not accept a decline in genetic level of any of the three main traits (fur quality, body weight and litter size).

Genetic Evaluation and Parameters

Genetic evaluation of fur animals is conducted within-herd using standard software created for this purpose. For fur animals this works quite well, because the entire breeding programme operates at herd level, and because genetic evaluations, and the assessment of environmental effects, are relatively simple when compared with those for other livestock species such as cattle and horses. Environmental influences on phenotypic performance can be considered homogeneous within herd, year, sex and parity.

Kopenhagen Fur provides a software package (FurFarm) for managing breeding to their members. The FurFarm system handles farmer records (performance results and other information about the animal such as its parents) and performs single-trait genetic evaluations using an animal model including a few environmental effects (sex and year) in addition to random effects of animal and permanent environment.

Along with FurFarm, a few other commercial systems are being marketed. The Morsø Winmink system is the alternative most often used in Denmark. It works in a similar way to the Kopenhagen Fur system, although it does perhaps use more approximate methods for genetic evaluation and mating proposals. A decisive factor for breeders is how flexible and user-friendly the software is; it is also important for the system to produce statistics that assist in the practical management of the population.

Table 1. Heritabilities (h^2) for different mink traits, as used in the FurFarm software

	h^2
November weight	0.40
Litter size	0.10
Fur quality traits:	
Quality	0.20
Colour (darkness shade)	0.25
Colour (pureness)	0.30
Pelt defects	0.30

We have limited knowledge of genetic correlations. However, unfavourable genetic correlations have been found between weight and pelt quality, as well as between weight and litter size (e.g. Lagerkvist et al., 1994). In practice unfavourable genetic correlations are handled by attaching appropriate relative weights to the relevant traits.

Organization and Breeding Programme

The breeding programmes are organized within-farm, as mentioned above. This flat breeding system, which is unique among domesticated animal species, is due to the relatively low reproductive rate of males in fur animals and the rapid changes in demand for different kinds of fur product. As a result of the flat breeding structure any genetic progress achieved at one farm is spread relatively slowly to the rest of the population. Hence, there is also a considerable variation in genetic levels at different farms (about the same genetic variation between farms as within). Also, inbreeding is mainly a problem within herds, and it can usually be alleviated by buying new breeding animals from another herd. However, care should be taken where new breeding animals are always purchased from the same farm, as they may be genetically related to previous breeding animals in this case.

Although breeding programmes are run on a within-farm basis, a limited exchange of animals between farms does exist — e.g. to avoid inbreeding or introduce new lines. However, objective selection across farms is difficult due to the lack of across-herd breeding values. Instead fur farmers rely on customized top lists ('Hit-lists') produced by Kopenhagen Fur (web service). These lists give details of farmers receiving the highest prices per pelt and with superior performance, and of nearby colleagues having the desired type of animals. For several reasons the Hit-list cannot be relied upon to optimize breeding decisions: (1) average prices and other performance parameters are influenced by the environment and other non-genetic factors; (2) the lists do not account for animals being sold for breeding rather than pelting, which disadvantages farms that sell many of their best animals; (3) a farm average is not necessarily indicative of the breeding value of selected (e.g. worst) animals at the farm. It would seem fairly easy to extend and adapt the Kopenhagen Fur system so that it gives across-farm evaluations — at least, for farms which (a) are genetically linked because, for example, they have exchanged breeding animals, (b) measure traits in a similar way, and (c) can provide unique animal identifications. Of these conditions, it is (b) that presents the main obstacle, since certain traits (e.g. fur quality) may well not be measured in the same way on different farms.

The FurFarm and Morsø Winmink software systems provide mating proposals that help to avoid the mating of closely related animals and hence control inbreeding. However, many farms do not keep proper records of their animals. Some of these use a rotation system to reduce inbreeding, where they use males born in barn 1 in barn 2, males born barn 2 in barn 3, and so forth. This strategy is quite effective in controlling inbreeding when applied systematically.

The selection process can vary between farms, but the number of selected males and females is a function of the expected number of offspring per animal and the desired number of animals for the coming year. Thus, if a farmer has room for 10 000 mink in the coming year (same as current year) and expects 5 surviving pups per Female, he needs to select 2000 breeding females (40% of female pups born corresponding to a selection intensity of 0.97). Likewise he needs to select 400 males (8%, i=1.86) to maintain the population.

The selection is conducted in different steps, and there is usually a significant pre-selection of pups before the final selection in November. This pre-selection is an overall subjective assessment by the farmer. It is usually based on the animal's own phenotype, but in case of pelt gnaw, siblings and the dam are also often discarded. Normally the best females are kept for 2–3 seasons and the worst ~1/3 of the females are culled after their first season. The males are typically culled straight after mating, as they still have their winter fur in late March (i.e. they are only used for one season).

Examples of Genetic Trends

In Denmark the average litter size of mink has increased from 3.6 kits in the early 1970s to 5.5 kits in 2009. Likewise, the November weight has increased considerably. The proportion of 'large' pelts sold at Kopenhagen Fur between 1998 and 2005 increased from 24% to 78% for males, and from 44% to 89% for females. Breeding played a considerable role in bringing about these improvements; however, it is not known precisely how much of the gain was brought about by an improved environment.

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Useful homepages:

www.kopenhagenfur.dk/avler

www.iftf.com

www.efba-eu.com

Sheep Breeding

Hans Ranvig, Jørn Pedersen & Thomas Mark

Introduction

The main purpose of sheep farming in Denmark is lamb meat production. Most breeds also produce wool. However, normally the cost of shearing exceeds the market value of the wool in Denmark, although it does not do so in other countries such as Australia and New Zealand. Around the world there is also a significant market for sheep milk — mainly for cheese production and especially in Middle Eastern countries.

Worldwide there are about 1.1 billion (i.e. $\times 10^9$) sheep. The population has been fairly constant over the past couple of decades (FAO, 2008). Sheep are hardy animals, well suited to extensive animal production. They are often kept on land, such as mountainous terrain, which is unsuitable for other forms of agriculture. In Denmark sheep are often put to grass around fish farms, conifer trees and on grass seed fields after the harvest.

Denmark is a minor player in global sheep production. There are approximately 3000 small flocks with an average of 20 sheep per flock in Denmark. Only few of these (430 herds) participate in official performance-recording, and most of these recorded flocks are kept on small farms. In all ~8500 lambings are recorded each year in Denmark, but this equates to only 18 lambings (30 lambs) per herd on average. There are only a few big commercial flocks with up to 2400 ewes; these graze permanent grass pastures in the summer, and after weaning the lambs and ewes are allowed to graze on grass seed fields after the harvest.

Figure 1. A large flock of Texel ewes on a grass seed field after the harvest (photo: Jesper Rasmusen)

Both ram and ewe lambs are able to reproduce at 6 months old, but most often the ewes will lamb for the first time as two-year-olds. Most breeds produce 1.5 lambs per ewe per year. The lambs can be weaned at 3 months of age. One ram can mate with up to 100 ewes in a breeding season. Gestation lasts approximately five months.

Breeds

A vast range of breeds and crosses are used around the world: for example, 282 breeds are described at http://www.ansi.okstate.edu/breeds/sheep. Just 25 breeds are represented in Denmark, however, where Texel, Oxford Down, Dorset, Shropshire and Suffolk are the numerically dominant breeds.

Here we focus on breeds used in Denmark for meat production. These can be divided into groups to reflect the special qualities that they contribute to a crossbreeding system. Soundness of mouth, feet and legs, and a dense, protective fleece are of primary importance, together with good body conformation, which is associated with a fat layer, as body reserves for winter survival are important in all breeds.

Ram breeds: These are specialized meat breeds. They have a relatively large growth capacity of up to 0.7 kg a day and can produce slaughter lambs with good carcass quality. The specialized breeds in Denmark are as follows (the number of recorded ewes in 2008 is given in parentheses after the breed name): Texel (1900), Dorset (800), Oxford Down (550) Suffolk (800) and Shropshire (1000). Sheep in the ram sheep group do well on improved and well drained grassland on mineral rich soil. It should be noted that Texel absorb more copper and phosphorous in the intestine from a given feed than all of the other breeds. This is an advantage when the feed contains low levels of these minerals, but it also increases the risk of poisoning and other disorders when the level of these minerals is high.

Dual purpose breeds: These are generally characterized by good mothering abilities, such as easy lambings, sufficient milk yield for raising lambs. They still maintain a relatively good growth capacity and have a medium carcass quality. The following breeds are typical for this category: Leicester (240), Marsh (250), Rygja (100), Dansk Landrace (325) and Såne (150).

Ewe breeds: These are specialized for lambing. Lambing is likely to be easier in these breeds since they have fairly narrowly placed shoulders combined with a large width in the pelvic region; the lambings normally result in very vigorous lambs. Breeds include Gotland Pelt (400), Spel (400), Iceland (70), Finnsheep (120) and Gute. All of these breeds belong to the group Nordic Shorttail sheep. The listed breeds, with the exception of Finnsheep, do well at a low stocking rates on natural vegetation on sandy soils. Finnsheep deviate from the other breeds in the group by having a very high level of fertility, possibly caused by a major gene. Texel×Gotland ewes are popular among commercial lamb producers in Denmark.

Dairy breeds: These are used to increase milk production. The lambs are weaned shortly after lambing and the milk is sold for cheese production. Breeds include Friesian (130) and Lacaune. These breeds are not widely used for crossbreeding, because they do not perform well under extensive conditions. Instead they are used for dairy production in intensive systems, and there are very few such herds in Demark.

Wool breeds: These sheep are used for wool production. In Denmark there are only a few Merino sheep, which have very thin wool fibres, imported from Tasmania.

Table 1. Economic values (Danish kr per trait unit) for different breeds

Traits (unit)	Texel	Suffolk	Shropshire	Oxford Down	Dorset	Nordic[1]
Litter size (no. lambs born)	572	367	310	344	345	345
Lambing interval (days)	0	0	0	0	-1.40	-1.40
Longevity at 5 year (days)	0.30	0.60	0.80	0.49	0.80	0.80
Maternal survival at birth (pct alive/100)	617	423	740	649	740	760
Maternal survival at 2 mth (pct alive/100)	667	457	800	702	800	821
Maternal lambing ease (points)	-129	-89	-155	-136	-155	-160
Maternal growth at 2 mth (g/day)	1.38	2.22	1.72	1.20	0.90	1.20
Direct survival at birth (pct alive/100)	542	1260	434	685	740	760
Direct survival at 2 mth (pct alive/100)	586	1361	470	741	800	821
Direct lambing ease (points)	-114	-264	-92	-144	-155	-160
Direct growth at 2 mth (g/day)	1.38	0.93	1.75	1.11	0.90	1.20
Carcass form (EUROP points)	42	76	60	38	65	0
Scanning, fat depth (mm)	-11.4	-13.1	-35.0	-20.0	-41.5	0.0
Front end[2] (points)	6.53	1.43	1.43	4.20	1.40	1.50
Top line[2] (points)	13.05	2.93	2.93	8.33	2.80	3.00
Rump[2] (points)	13.05	2.93	2.93	8.33	2.80	3.00
Thighs[2] (points)	19.58	4.35	4.35	12.53	4.20	4.50
Legs[2] (points)	9.81	2.18	2.18	6.23	2.10	2.25
Type[2] (points)	6.53	1.43	1.43	4.20	1.40	1.50

[1]Nordic breeds comprise Gotland Pelt, Danish Spel, Gute, Icelandic, Finewool and Faeroe sheep

[2]Linear conformation score = 1, 2, … 9

Breeding Goal

The S-index reflects the breeding goal adopted by the relevant breed association. Table 1 shows the economic weights in the S-index for selected breeds in Denmark.

Genetic Evaluation and Parameters

The Danish Knowledge Centre for Agriculture in Skejby is responsible for calculating breeding values for sheep. For this purpose they use farmer records of lamb mortality (required), lambing ease (voluntary), litter size (required), birth weight (voluntary), weight at 2 months (voluntary) and weight at 4 months (voluntary). In addition to this, ultrasonic scannings of Longissimus Dorsi muscle and fat depth, as well as conformation scores performed by trained technicians, are used. The latter is not widely performed, whereas 10–20% of lambs are scanned for the beef breeds. The small number of records means that the breeding values of most animals have low accuracy. Old carcass records from slaughter houses are also still used, although new records have not been added since 2006, because carcass traits measured at slaughter are genetically correlated with similar traits measured by scanning living animals.

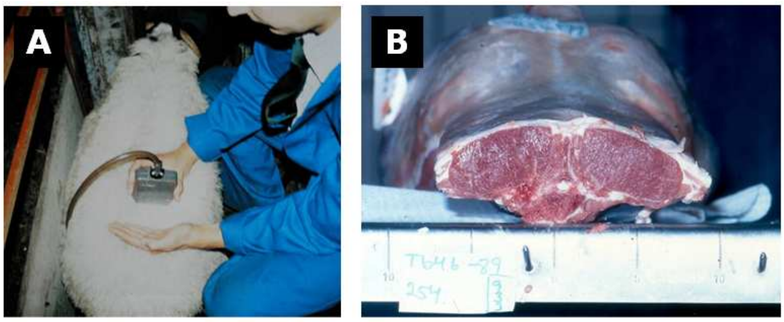

Figure 2. Ultra sound scanning (A) and Longissimus Dorsi cut from Texel (B). Photos from Hans Ranvig.

Breeding values are estimated using multi-breed Animal Models. Explanatory environmental effects considered vary from trait to trait, but often include interactions of breed with herd×year, sex, season, and age, as well as permanent environment. Both direct and maternal genetic effects are included in the models to account for the effects of both the lambs own, and the mother's, genetic make-up, respectively.

Genetic parameters have recently been estimated by Maxa et al. (2005, 2007, 2008, 2009) and by Norberg et al. (2005, 2006). These estimates, combined with commonly used genetic parameters in sheep breeding, form the basis for the estimation of breeding values. The assumed heritabilities and phenotypic standard deviations are listed in Table 2. Genetic correlations of 0.8 and 0.7 are assumed between growth rate at 2 and 4 months of age (maternal and direct, respectively), 0.65 between carcass form score and muscle depth, and 0.5 between carcass fat score and fat depth. Furthermore longevity at 1, 3 and 5 years of age are highly correlated genetically (0.86–0.96).

Table 2. Heritabilities (h^2) and phenotypic standard deviations (σ_p) of evaluated traits

Trait (unit)	h^2	σ_p
Litter size (no. lambs)	0.100	0.55
Lambing interval (days)	0.025	100
Survival at birth, direct (pct alive/100)	0.08	0.17
Survival at birth, maternal (pct alive/100)	0.04	
Survival at 2 mth., direct (pct alive/100)	0.04	0.10
Survival at 2 mth, maternal (pct alive/100)	0.04	
Lambing ease, direct (points)	0.03	0.63
Lambing ease, maternal (points)	0.06	
Longevity, 1 year (days)	0.03	37
Longevity, 3 year (days)	0.04	134
Longevity, 5 year (days)	0.05	313
Growth rate, 2 mth., direct (g/day)	0.23	54
Growth rate , 2 mth, maternal (g/day)	0.13	
Growth rate, 4 mth, direct (g/day)	0.19	48
Growth rate, 4 mth, maternal (g/day)	0.11	
Carcass, form score (EUROP points)	0.40	1.5
Carcass, fat score (EUROP points)	0.13	0.49
Muscle depth., scanning (mm)	0.33	2.1
Fat depth, scanning (mm)	0.17	0.78
Conformation traits (points)	0.16	1.0

Health traits are not included in the S-index. Examples of genetic impact on health are found in resistance to parasites and scrapie. Heritability for resistance to internal parasites like *Haemonchus* is about 0.3. Resistance to myasis is about 0.25. Resistance to scrapie receives considerable attention in other countries, such as the United Kingdom, where scrapie is a major problem. A major gene that controls scrapie has been found, and a genetic test is available. The test is not used by Danish sheep farmers, except when it is required for exporting, as Denmark is declared scrapie free. Sheep that are homozygotic for the allele ARR have a very high degree of resistance to the prion which causes the disease. The prion has an effect on the central nervous system similar to that witnessed in BSE in cattle. Heterozygotic sheep with one ARR and no VRC allele are partially resistant to this effect.

Marker assisted selection is not used in Danish sheep breeding, although some knowledge of single genes exists. The Callipygian gene is an example of a single gene that has a markedly positive effect on carcass quality. The presence of this gene results in increased dressing of 5–8%, increased loin eye area of 22–34%, and decreased depth of fat on the back of 25–32% . Despite the general improvement in carcass quality it causes, this gene has a significantly negative effect on meat quality.

Coat colour is a quantitative trait that is important from the standpoint of breed. It is determined by one or a few pairs of genes with a sharp distinction between phenotypes.

Autosomal recessive defects are rarely seen today, because breeding programmes are designed to exclude them. Examples of such defects are inherited blindness in Texels, ‘naked lambs’ (an inherited disorder of thyroid metabolism) in Dorsets and Merinos, and cleft palate in Shropshires.

Organization and Breeding Programmes

There is no properly organized overall plan in Danish sheep breeding, although there have been several attempts to establish one. From a theoretical standpoint it could be claimed that if breeders use animals with a high S-index for breeding, they are following a de facto breeding plan. However, often breeders prefer to base their selection decisions on their own subjective assessments. The breeders are proud of their stock and sometimes rely on old customs based on intuition. This may work well for highly heritable traits such as growth and muscle depth, but it is less effective for less heritable traits such as litter size, lambing ease, lamb vitality and longevity.

Most breeders avoid mating closely related animals. Due to this, and the fact that much selection emphasis is based on phenotypes rather than breeding values, inbreeding is typically not considered a problem in Danish sheep breeds. Norberg and Sørensen (2006) estimated inbreeding rates for the past decade of 1.0–1.1% for Texel, Oxford Down and Shropshire, which is an acceptable inbreeding rate. Inbreeding may be more of a problem in smaller breeds, but this has not been investigated.

Ultrasonic scanning of the fat and muscle depth of the back muscle is mostly carried out in flocks of ram breeds. Linear conformation assessment is carried out in only a few flocks, and the data are included in the index for body conformation with a low economic weight. This may explain the limited interest in this breeding assessment.

Results from livestock shows are not integrated in the S-index, but these results carry a great deal of prestige for many breeders. Breeders who have obtained top results several times have a high status among colleagues and can use their reputation to sell breeding animals. Some breeders claim that the prizes they are awarded at the shows are the only benefit they get from their breeding work. However, marketing and social engagement are often the main reason for showing animals.

Examples of Genetic Trends

Table 3 shows the genetic trends of some of the most important traits for selected sheep breeds. More detailed data of this kind, including results on single animals, can be found at www.landbrugsinfo.dk/Faar-og-geder.

Table 3. Genetic change[1] per year for selected breeds and traits, average per year 2001–2010

	Oxford Down	Shropshire	Texel	Dorset	Suffolk
Litter size, number	0.0034	0.0069	0.0071	0.0013	0.0050
Longevity at 5 years, days	2.0	6.5	1.5	1.7	1.1
Maternal lamb survival at birth, %	0.01	0.25	0.16	0.17	-0.05
Direct lamb survival at birth, %	0.25	0.20	0.05	0.06	-0.02
Maternal growth rate at 2 mth, g/day	0.33	1.20	0.51	-0.43	-0.55
Direct growth rate at 2 mth, g/day	1.63	1.31	1.16	0.06	1.85
Muscle depth, mm	0.03	0.01	0.03	0.02	0.03
Thighs, point	0.002	-0.020	0.016	-	-

[1]The genetic trend is calculated as the regression of EBV on year of birth, and only animals born in 2001 and later are included

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Useful homepages:

www.landbrugsinfo.dk/faar-og-geder/

Horse breeding

Karina Christiansen, Maiken Holm, Jørgen Finderup & Thomas Mark

Introduction

Before industrialization the horse was an important provider of pulling power in the agricultural sector. Even in the 1940s there were about 600 000 horses in Denmark, but thereafter the numbers dropped to around 60 000 in the mid-1960s. Since then the horse has enjoyed a renaissance as sports and leisure animal, and today there are about 200 000 horses in Denmark. To put that figure in perspective, there are 59 million horses worldwide (FAO, 2008).

Today horses are used in many different ways. As well as being used for hobby and leisure, horses are ridden or driven in a wide variety of sporting competitions. They are also employed in less traditional areas such as health therapy, tourism and nature preservation. An analysis of the economic influence of the Danish horse sector was produced in 2010 showing a total turnover of 23 369 million DKK, and that 20 849 full time jobs have been created in and by the sector.

Horse breeding in Denmark is organized around the National Committee of Horse Breeding, which consists of representatives of 30 member breeding societies and covers more than 95% of the registered breeding horses. The committee deals with overall political and strategic matters within horse breeding, and seeks to establish common guidelines and rules for breeding and registration.

The equine section of the Knowledge Centre for Agriculture keeps the studbooks for the majority of breeding societies represented on the National Committee and maintains a *National Horse Database*.

Breeds

A wide variety of breeds are handled in Danish Horse breeding. They are traditionally divided into the following groups on the basis of shared, or somewhat similar, characteristics:

<u>Special breeds (group A)</u>. The group of special breeds consists of lighter, noble and specialized breeds. Several of them, including Frederiksborg, Lipizzaner and P.R.E., are baroque breeds with more than 400 years of history behind them. This group also contains highly specialized racing horses such as Thoroughbred and Trotters and the oldest breed in the world, Arabian Thoroughbred.

Other breeds in the group include Oldenburg, Pinto, Friesian, Shagya, sports and Anglo Arabians, Quarter Horse, Paint Horse, and Appaloosa.

Danish Warmblood – National riding horse (group B). The Danish Warmblood has been part of organized horse breeding in Denmark since 1962. Before this, there was no specialized, modern riding horse breeding in Denmark. The primary purpose of these horses is dressage and jumping competitions.

Draft horses (group C). The main goal for these heavy horses is to produce power for draft work. Therefore they need to be powerful horses, with a co-operative and willing temperament. Breeds here include Jutland horses, Belgian horses, Shire, and North Swedish Working Horse.

Smaller horses (group D1). Horses in this group have traditionally performed duties originally believed to be suited to larger horses. The group consists of horses with remarkable ‘original traits’ providing good fitness in natural environments, a good temperament and high health status. Today the group is mainly used as versatile hobby and sports horses. The breeds include Fjord, Icelandic horses, Haflinger, and Tinker (or Irish Cob).

Ponies (group D2). Pony breeds display broad variation in size and background, from the Danish Sports Pony (DSP), which represents breeding for specialized types of riding pony, to the English Mountain and Moorland breeds, to the Miniature Horses. Common to all is good temperament, making various kinds of use possible, and making these ponies a good starting horse for children. Breeds also include Connemara, New Forest, Dartmoor, Gotland Russ, Welsh Ponies and Shetland Ponies.

Breeding Goal

We shall focus exclusively on the horse with the largest horse breeding association in Denmark, the Danish Warmblood (DWB); breeding for the other breeds is less developed. DWB is an open studbook that uses many international warmblood breeds to produce riding horses of a specifically defined type and function. It is an advantage of an open studbook that inbreeding is easier to control.

The present breeding objective of DWB is: ‘A noble, leggy and supple riding horse with high rideability and a strong health. It has capacity in either jumping or dressage to compete at international level”.

Before 2004 the breeding goal of DWB was to produce all-round sport horses that were able to compete in both jumping and dressage competitions. However, in 2004 the studbook initiated a division of the breed into dressage and jumper specializations, because the genetic correlation between the two functional qualities was estimated to be negative (Nielsen & Pless, 2007) and because there was a growing demand among riders for specialized horses. The population now consists, approximately, of 65% dressage-adapted horses and 35% jumping-adapted horses.

Figure 1. The breeding goal for Danish Warmblood is to breed horses that excel in either dressage or jumping as illustrated here by Hønnerups Driver (left) and Toftehøjs Credeau (right), respectively (photos by Wiegaarden)

With horses it is difficult to estimate economic values for each trait, as many approach horse breeding as a hobby and have no, or very low, expectations of profit; again, the market value of a horse is often influenced by fancy. As a result of this, DWB does not have a total-merit breeding goal of the sort that combines all traits in a single index, although sub-indexes of young horses for jumping and dressage are published. The unavailability of a total-merit index makes focused, systematic breeding difficult and leaves the difficult decision of weighing traits against each other to individual breeders.

In her master’s thesis, Mia Haagensen investigated the realized selection emphasis of an ‘average’ DWB breeder by correlating breeding values of stallions for dressage, jumping and conformation with the subsequent increase in numbers of progeny. This work revealed that breeders put equal selection emphasis (selection index weights) on dressage and conformation, and twice as much emphasis on dressage than they do on jumping.

Health and longevity are also part of the breeding goal, but currently breeding values are missing for these traits and there is no direct selection emphasis on them other than natural selection (and some phenotypic selection against health disorders such as osteochondrosis). Typically, a riding horse is 9–11 years old before its performance peak. By then, many years of intensive training have been spent on the horse, so longevity is a crucial quality. DWB has recently started to collaborate with Danish veterinarians on pathological registration. In the future, veterinary diagnoses will be uploaded to the Danish horse database so that the information can be utilized in future selection procedures.

Genetic Evaluation and Parameters

DWB has four main categories of estimated breeding value (EBV) corresponding to different age groups:

1) EBVs for competition traits (dressage and jumping; ≥5 year-olds)
2) Championship EBVs (4-6 year-olds)
3) Young Horse EBVs (3-4 year-olds)
4) EBVs for conformation traits

Competition EBVs are based on results registered with the Danish Equestrian Society. Horses are typically 5 years or older when they first receive a competition EBV. Therefore the Young Horse, Championship and conformation EBVs are important if earlier selection is to take place. Young Horse EBVs are based on results from saddle grading, station tests, and ability tests of horses that are generally 3 or 4 years old. Young Horse and Competition EBVs are combined into a weighted average known as a Total EBV for both dressage and jumping traits. EBVs for conformation traits from all judgements on mares and stallions in the DWB are carried out. There is no aggregate EBV for conformation. Instead the trait 'general impression' is used to rank overall conformation.

Genetic evaluations are conducted once a year. All EBVs are standardized to indices with a mean of 100 and a standard deviation of 20 before publication. A rolling base is used, so that the mean and SD refer to an updated reference group for each new evaluation.

A certain level of accuracy is required before an EBV can be published. Young Horse and competition EBVs for stallions are published when they have at least 15 informative offspring. For mares, Young Horse EBVs are published when the mare (or at least one offspring) has been tested in saddle grading, a station test, or an ability test. The competition EBV for mares is published if the mare (or at least one offspring) has at least five competition results.

The Estimation of Competition EBVs

Rankings in competition (transformed with a square root) are used as a dependent trait for dressage and show-jumping evaluations. The two traits are analyzed separately using single trait repeatability animal models with the following explanatory effects: level of competition measured as class×venue×year (fixed), gender×age (fixed), rider category (fixed), permanent environment (random), animal (random), and residual (random). The rider category has three levels, and these are defined as follows: riders have competed at national elite competition (category 1); a national competition (category 2); another competition at a lower level (category 3).

Heritabilities are low for competition traits, especially jumping (Table 1). This may be due to the fact that older horses have been trained over a longer period of time, so that the rider's influence on the horse increases. Training is one of the most difficult environmental factors to separate from other environmental effects.

Table 1. Genetic parameters for competition traits (Crolly, 2010a)

Parameters	Dressage	Show Jumping
Heritability	0.21	0.11
Repeatability	0.37	0.21
Genetic variance[1]	0.26	0.28
Phenotypic variance[1]	1.22	2.56

[1]Expressed on transformed scale, i.e. in ranking units

The genetic correlation between dressage and show jumping has been approximated at 0.66 (Nielsen & Pless, 2007).

The Estimation of Championship EBVs

Championship traits are judged using a scale of 1–10, where 10 is the highest score and signals the breed objective. Multiple-trait animal models are used to evaluate each of the following groups of traits (traits in different groups are analysed separately):

1. Gaits with five traits: walk, trot, canter, rideability and capacity.
2. Jumping (single trait since 2010; previously 3 traits)

Both models include the following explanatory effects: Place×date (fixed), age (fixed), breed proportion (fixed), heterosis (fixed), rider (random), permanent environment (random), animal (random) and residual (random). Heritabilities are 0.16 for walk, 0.30 for trot, 0.25 for canter, 0.11 for rideability, 0.23 for capacity and 0.09 for jumping.

The Estimation of Young Horse EBVs

Young horse traits are judged using a scale of 1–10, where 10 is the highest score and signals the breed objective. Multiple-trait animal models are used to evaluate each of the following groups of traits (traits in different groups are analysed separately):

1. Gaits with seven traits: walk, trot, canter, rideability, capacity, and rideability and capacity with test rider
2. Free-jumping with three traits: capacity, technique, canter
3. Jumping with rider with four traits: capacity, technique, canter and rideability

Each of the three models includes the following explanatory effects: Place×date (fixed), gender×age (fixed), breed proportion (fixed), heterosis (fixed), animal (random) and residual (random). Data from 1984 onwards are considered in the evaluations. EBVs for the first group of traits are combined into a Young Horse Dressage Index with the following index weights:

$$0.25(EBV_{walk}) + 0.2(EBV_{trot}) + 0.25(EBV_{canter}) + 0.2\times[0.5(EBV_{rideability}) + 0.5(EBV_{rideability,\ test\ rider})] + 0.1\times[0.5(EBV_{capacity}) + 0.5(EBV_{capacity,\ test\ rider})]$$

Similarly, EBVs for the second and third groups of traits are combined into a Young Horse Jumping Index with the following index weights:

$$0.3(EBV_{rideability}) + 0.3\times[0.5(EBV_{capacity,\ free\text{-}jumping}) + 0.5(EBV_{capacity,\ with\ rider})] + 0.3\times[0.5(EBV_{canter,\ free\text{-}jumping}) + 0.5(EBV_{canter,\ with\ rider})] + 0.1\times[0.5(EBV_{technique,\ free\text{-}jumping}) + 0.5(EBV_{technique,\ with\ rider})]$$

Genetic parameters used in the three multiple-trait genetic evaluations are shown in Tables 2, 3 and 4. Heritabilities for young horse dressage traits are moderate to high (Table 2), as has been found for foreign warmblood populations. Genetic correlations between the dressage traits are generally high (0.55–0.98). The highest correlation is that between the scores for rideability and capacity given by the test rider and the judges on the ground (0.97 for rideability and 0.98 for capacity). Consequently, the studbook has discussed the possibility of making no further use of a test rider; so far, however, political support has not been forthcoming.

Heritabilities for young horse jumping traits are low to moderate, the lowest being jumping with rider. The cause of this may be that, through training, it is easier to change a horse's jumping abilities than its basic gaits, and that training is difficult to adjust for effectively in the statistical model. The genetic correlations between jumping traits are generally higher than those between dressage traits.

Table 2. Genetic parameters for young horse dressage traits (Boelling, 2010)

	Walk	Trot	Canter	Rideability	Capacity	Rideability, test rider	Capacity, test rider
h^2	0.32	0.48	0.41	0.25	0.46	0.25	0.41
σ^2_a [(1)]	0.25	0.37	0.25	0.16	0.27	0.19	0.27
Genetic (above diagonal) and residual (below diagonal) correlations:							
Walk		0.55	0.55	0.63	0.73	0.54	0.66
Trot	0.24		0.80	0.86	0.94	0.74	0.96
Canter	0.27	0.48		0.84	0.91	0.73	0.87
Rideability	0.26	0.36	0.41		0.91	0.97	0.96
Capacity	0.54	0.66	0.67	0.46		0.79	0.98
Rideability, test rider	0.13	0.23	0.25	0.50	0.26		0.88
Capacity, test rider	0.22	0.37	0.35	0.27	0.40	0.46	

[1]Expressed in points^2, where the points refer to the scale 1, 2…, 10 points used for classification

The correlation between technique and capacity is especially high, indicating that these are measures of the same trait. In the set of data used dressage, as well as jumper, mares have been judged. Since from now on only jumper-adapted mares will obtain jumping scores it is likely that the differentiation between technique and capacity will increase.

Table 3. Genetic parameters for young horse free-jumping traits (Boelling, 2010)

	Capacity	Canter	Technique
h^2	0.33	0.22	0.27
σ^2_a	0.41	0.20	0.32
Genetic (above diagonal) and residual (below diagonal) correlations:			
Capacity		0.79	0.97
Canter	0.65		0.92
Technique	0.66	0.66	

[1]Expressed in points^2, where the points refer to the scale 1, 2…, 10 points used for classification

Table 4. Genetic parameters for young horse jumping with rider traits (Boelling, 2010)

	Rideability	Capacity	Canter	Technique
h^2	0.14	0.26	0.14	0.13
σ^2_a	0.15	0.31	0.12	0.17
Genetic (above diagonal) and residual (below diagonal) correlations:				
Rideability		0.96	0.88	0.99
Capacity	0.69		0.69	0.98
Canter	0.67	0.76		0.83
Technique	0.70	0.86	0.74	

[1]Expressed in points^2, where the points refer to the scale 1, 2…, 10 points used for classification

Estimation of Breeding Value for Conformation

Conformation traits are judged using a scale of 1–10, where 10 is the highest score and signals the breed objective. The most frequent scores are 6–8. Judgements are subjective, so two or more judges work together and as much as possible, with consistent use of the same judges at different evaluations. All conformation traits have been recorded since 1984 in seven different judging regions in Denmark.

A single-trait animal model is used for the genetic evaluation of each of the conformation traits. The models include the following explanatory effects: Year (fixed), region (fixed), animal (random) and residual (random).

Heritabilities tend to be higher for conformation (Table 5) than performance traits, because no rider and only limited training is involved in conformation. Due to this, and because of the early registration, conformation traits are valuable as indicators of later performance. The heritabilities for legs are lower, probably as a consequence of complex trait definition and scoring.

Table 5. Genetic parameters for conformation (Crolly, 2010b)

Traits	h^2	σ^2_a
Type	0.46	0.44
Shoulder and withers	0.41	0.44
Topline	0.38	0.44
Fore legs	0.23	0.17
Hind legs	0.28	0.21
Gaits shown loose	0.45	0.40
General impression	0.50	0.49

[1]Expressed in points^2, where the points refer to the scale 1, 2…, 10 points used for classification

Genetic Correlations among Competition Traits and Early Indicator Traits

Information on performance traits becomes available late in the horse's life, and efficient selection is further complicated by low heritabilities for those of these traits of main interest. Data on conformation and traits recorded at young horse tests are available earlier, and these traits are generally more heritable. Conformation can be recorded already in foals. Thus, these traits are useful as indicator traits and can help the breeder to achieve correlated genetic progress if they are strongly correlated with performance traits, genetically. Nielsen & Pless (2007) estimated genetic correlations among all traits in the DWB breeding programme using an approximate method. They found, for instance, that the genetic correlation between canter and jumping was moderate to high (0.27 to 0.98). Therefore, canter can be used in early selection for jumping abilities.

The genetic correlations between traits recorded at young horse tests and performance traits are high for both dressage and jumping (~0.8). Genetic correlations between dressage and conformation traits are moderate to high (0.16–0.89). Some conformation traits are therefore well-suited as an indirect selection of dressage performance. Genetic correlations between jumping and conformation traits are also positive, but lower (0.04–0.49). This means that conformation traits are more useful for improving dressage performance, while young horse tests are more important for improving jumping performance.

Organization and Breeding Programme

Selection is strongest on the paternal side. This is because single stallions, through AI, can make considerable contributions to the breed, whereas mares have, on average, only 3.4 offspring, leaving little room for selection among mares if population size is to be maintained. The breeding typically centres on a few popular stallions. Annually, around 7 stallions are used in approximately 30% of the 4000 coverings. These 7 stallions cover more than 100 mares each. Approximately 20% of the coverings involve roughly another 10 stallions, with each covering 50–99 mares. The remaining 50% of coverings are normally distributed over approximately 170 stallions, with each covering fewer than 50 mares.

Selection System for Stallions

DWB has a stringent procedure for selecting stallions on the basis of their own phenotypic performance, although selection on breeding values is known to be more efficient than phenotypic selection. All stallions used for breeding must have passed an approved riding test that identifies high rideability and extraordinary competition skills. Foreign stallions that have not had a Danish riding test can be accepted if the stallion fulfils certain requirements (i.e. performs well in an accredited foreign riding test and has good conformation). If a breeder wishes to use a foreign stallion an application must be send to the DWB association for each desired mating. About 300 applications are received each year; most are accepted.

Table 6 gives an overview of selection systems for stallions. The first requirement in the first selection step is sufficient information completeness regarding ancestors. Each ancestor for at least four generations back must have been judged, and both parents must have passed a riding test. At the pre-selection of colts in November about 60 out of 250 individuals are selected for the stallion show in March, where approximately 20 young stallions are licensed. More than half of the 250 colts are usually of foreign origin (having been imported into Denmark at a young age). Good conformation is more important for dressage than jumping, and different conformation traits are important. Prior to breeding, horses have to pass a 10-day observation test that starts the day after the licensing. They are observed primarily for temperament, rideability and potential hereditary defects, like roaring. If the stallions pass the test, they are given a one-year covering permission. Before it enters the stallion list the horse's health and fertility is checked by a veterinarian; a DNA test is used to verify its pedigree.

After the first breeding season, the young stallions can enter a 35-day test where their dressage and/or jumping performance is evaluated. If they pass with a score of at least 800 out of 1000 points they are allowed to enter for final grading the following year. If their score is between 700–800 points they are offered the opportunity to get through to final grading either through another 35-day test the following year or through high-class performance in the young horse championships for horses of 4 to 6 years old. Older stallions with excellent results in international competitions may also be accepted for final grading, but this route involves only one or two stallions a year. Generally, just 1% of the colt foals end up as finally approved stallions. A few of the finally graded stallions are later appointed Elite stallions on the basis of very good breeding results, where the stallion must conform to special rules.

Table 6. Selection steps and corresponding number of selection candidates (N) for stallions; information sources and selection intensity at different ages

Selection step	Age (yr)	Dressage stallion selected on	Jumping stallions selected on	N
Pre-selection	2½	▪ Information completeness of ancestors ▪ Conformation ▪ Gaits shown loose	▪ Information completeness of ancestors ▪ Conformation ▪ Free jumping and canter	~ 250
Stallion show	3	▪ X-ray and soundness ▪ Height (min. 1.62) ▪ Conformation ▪ Gaits shown loose and in lungeing reins	▪ X-ray and soundness ▪ Height (min. 1.62) ▪ Conformation ▪ Free-jumping and canter shown in lungeing reins	~ 60
10 days observation test	3–5	▪ Temperament ▪ Rideability ▪ Hereditary defects	▪ Temperament ▪ Rideability ▪ Hereditary defects	~ 20
35 days test	3–5	▪ Dressage ability under rider and test rider	▪ Jumping ability under rider and test rider and in free–jumping	~ 20
Final grading (stallion show)	4–?	▪ Development ▪ Results from performance test	▪ Development ▪ Results from performance test	~ 15
Elite stallion	older	Good breeding results and own performance		~ 2

Selection System for Mares

The selection intensity of mares is near zero. Also, it is problematic for breeders that many of the best mares are used for competitions before being used for breeding.

However, approximately 1200 mares of 3 years old or more are phenotypically evaluated at mare grading each year. Ordinarily, very few such mares (<5) each year obtain a score below 5 in 'general impression' and are, on that basis, refused permission to enter the breeding programme. The successful mares are divided into various classes, depending on their pedigree and quality; and the breeders themselves decide whether a mare should be used for breeding (Table 7).

Around 600 of the 1200 mares are also tested under rider at a saddle grading, a station test or an ability test. An approved riding test and grading in Dansk Hovedstambog (DH) or Dansk Stambog (DS) is a condition of becoming a stallion mother. Approximately 50 of the best mares with a riding test and DH grading are selected for the elite mare show in early September. On the basis of very good breeding and competition results older mares can be appointed Elite mares. By 2010 only 592 mares had been appointed Elite mares.

Table 7. Selection steps for mares

Class	Criteria	Pct. Selected[1]
DH (Main studbook)	▪ Pedigree: judgement in at least three generations ▪ Height of min. 1.60 m ▪ Min. 8 in 'general impression'	40%
DS (studbook)	▪ Pedigree: judgement in at least every second generation ▪ Height of min. 1.55 m ▪ 6 or 7 in 'general impression'	50%
DR (studbook register)[2]	▪ Pedigree: judgement in at least every second generation ▪ Height of min. 1.48 m ▪ Min. 5 in 'general impression'	3%
FOR (supplementary studbook)	▪ Unknown pedigree or judgement in less than three generations (F1, F2 or F3) ▪ Height of min. 1.48 m ▪ Min. 5 in 'general impression'	7%

[1] Of ~1200 mares
[2] DR = Dansk Register

DWB works with a wide range of grading and quality tests of mares, as summarized in Table 8. All but the station tests are one-day events. At the station tests the mares are taken care of and trained under uniform condition for about 30 days, which ensures a fairer evaluation of the mare's own abilities (rather than those of its trainer).

Table 8. An overview of the mare grading possibilities

Mare grading possibilities	Dressage mares selected on	Jumping mares selected on	No. of mares
Exterior evaluation (one day)	▪ Pedigree + height ▪ Conformation ▪ Gaits shown loose	▪ Pedigree + height ▪ Conformation ▪ Free-jumping and canter	~ 600
Saddle grading (one day)	▪ Pedigree + height ▪ Conformation ▪ Dressage ability under rider and test rider	▪ Pedigree + height ▪ Conformation ▪ Free jumping ▪ Canter and rideability under rider and test rider	~ 460
Station test (30 days)	▪ Pedigree + height ▪ Conformation ▪ Dressage ability under rider and test rider	▪ Pedigree + height ▪ Conformation ▪ Free jumping ▪ Canter and rideability under rider and test rider	~ 40
Ability test (one day – only 4-year-old mares and registered geldings)	▪ Pedigree + height ▪ Conformation ▪ Dressage ability under rider	▪ Pedigree + height ▪ Conformation ▪ Free jumping + jumping under rider ▪ Canter and rideability under rider	~ 100

Examples of Genetic Trends

Genetic trends for dressage, show-jumping and the conformation trait ‘general impression’ are shown in Table 9. The trends are highest for conformation and dressage. The genetic progress for jumping was less than could potentially have been achieved. The trend calculations were based on EBVs obtained in 2008 for 311–414 stallions. The weighted trends reflect the total genetic progress of the population; the un-weighted trends illustrate the success of selecting stallions for approval.

Table 9. Genetic trends[1] (± SE) per year and per $0.01\sigma_a$ (either weighted by no. progeny or un-weighted) for stallions of all ages and those born after 1984 (from Mark et al., 2010)

	Weighted		Un-weighted	
Trait	All ages	born after 1984	All ages	born after 1984
Dressage	5.5 ± 0.5	9.9 ± 1.2	3.8 ± 0.5	6.7 ± 1.0
Show-jumping	2.9 ± 0.6	-2.0 ± 1.7	2.0 ± 0.5	1.2 ± 1.3
General impression	8.1 ± 0.3	5.6 ± 0.7	7.8 ± 0.3	3.7 ± 0.7

[1]Regression coefficients (b) from regression of birth year on breeding value; model: $EBV/\sigma_a = a + b(year)$.

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Dog Breeding

Merete Fredholm & Helle Friis Proschowsky

Introduction

The history of the domestic dog can be traced back at least 15 000 years and possibly as far back as 100 000 years [e.g. 1, 2, 3]. The earliest archaeological evidence of a domesticated dog is a mandible from a grave at Oberkassel in Germany; it is 14 000 years old [4]. However, archaeological findings tend to underestimate the period of domestication, and an analysis of the mitochondrial DNA of the mandible implies that the origin of the dog is considerably more ancient. Dogs evolved from the grey wolf through various advances in domestication involving repeated genetic exchanges between dog and wolf populations. Domestication has been accompanied by a variety of human needs for assistance with, for instance, herding and hunting (see further details below in section about 'breeds'). Selective breeding over recent centuries has ensured that dogs now display tremendous variation in their behavioural, physiological, and morphological phenotypes, resulting in over 400 genetically distinct breeds. As Fig. 1 illustrates, dogs exhibit a huge variation in body size — indeed greater variation in this respect than any other terrestrial mammal species.

Figure 1. Example of variation in body size in different dog breeds (Yorkshire Terrier puppies, Yorkshire Terrier, Pomeranian and Dogue de Bordeaux, respectively).

It is not easy to establish an accurate estimate of the total number of dogs worldwide — for instance, the number of stray dogs in Delhi, India is thought to be 200 000. The five countries in the world with the largest dog populations are: USA: 60 million; Brazil: 30 million; China: 22 million;

Japan and Russia: 10 million each. In Denmark dog registration is statutorily required. All dogs must be registered in the 'Dansk Hunderegister' (Danish dog registry). The Danish dog population comprises approximately 550 000 dogs of which 60–70% are purebred; so the remaining 40–30% of Danish dogs are crossbred.

Sexual maturity in the dog develops at 6–12 months (with the latest arrival occurring in large dogs). Pregnancy is possible in the first oestrus cycle, but breeding is not recommended before the second cycle. The average length of the reproductive cycle for females is 6 months. Dogs bear their litters roughly 9 weeks after fertilization, although the length of gestation can vary from 59 to 65 days, with 63 days being the average. The average litter size is about 6 puppies, but the number varies greatly between breeds. Toy dogs, for instance, produce 1–4 puppies, while larger breeds may average as many as 14 puppies per litter.

Breeds

The first evidence of distinctive breeds of dog dates to 3000 years ago in ancient Egypt. Early Egyptian art illustrated two types of dog: one that was slender with erect ears and a curly tail; and another that was shorter with a heavy muzzle and drop ears. Since then, a broad variety of breeds have been developed, ranging from the diminutive Chihuahua to the giant Irish wolfhound. The more than 400 breeds that are recognized worldwide are traditionally divided into 10 groups according to their morphological or functional characteristics. The 10 groups are also used in dog shows and competitions.

Group 1 Sheepdogs and Cattle-Dogs. Breeds like the German Shepherd, the Belgian Sheepdog, the Collie, the Shetland Sheepdog, the Border Collie and the Old English Sheepdog are included in this group. The original use of these breeds was to help the shepherd when he was gathering his flock together or when he wanted to move the flock to another grazing area. The sheepdogs are agile and alert dogs, and today many of them perform very well in competitions involving agility or obedience.

Group 2 Pinschers, Schnauzers and Molossoid Breeds. Group 2 is more diverse, ranging from small pinchers to the heavy Mastiff types of dog originally used to guard homes and property. The group also includes the guarding shepherd breeds like the Bernese Mountain Dog, the Saint Bernard, the Leonberger, and the Pyrenean Mountain Dog. Popular breeds like Boxers and Newfoundlands, and the national Danish dog breed, the Broholmer, are also in group 2. The Schnauzers come in three sizes: miniature, standard and giant.

Group 3 Terriers. The terriers were originally used for hunting, but today they are mostly companion and family dogs. Most of the terriers have wirehair coat that offers good protection from the elements.

Group 4 Dachshunds. The dachshunds were developed for hunting foxes and badgers out of their earths and setts. They belong to the so called 'chondrodystrophic' breeds. This term is used to characterize the phenotypical shortness of leg caused by an inherited type of dwarfism. Dachshunds come in three hair-variants (smooth-haired, long-haired and wire-haired) and three size variants (standard, miniature and rabbit).

Group 5 Spitz Dogs and Primitive Types. The Nordic spitz dogs, like the Greenland Dog and the Siberian Husky, were originally used to pull sledges. Spitz dogs like the Norwegian Elkhound were also used for hunting. The primitive types include breeds like the Mexican and Peruvian hairless dogs and the Basenji.

Group 6 Scent Hounds and related breeds. The Bloodhound, the English Basset and the Beagle belong here, as do the French Basset types. Norway and Sweden have a number of national breeds in this group as well — for instance, the Hygen, Hamilton and Schiller Hounds and the Swedish Drachsbracke.

Group 7 Pointing Dogs. Pointing dogs are used for hunting. They include breeds like the Pointer, the English and Irish Setters and the German smooth-haired or wire-haired Pointers. They all have the ability to 'freeze' in a pointing or setting gesture when they identify a bird or other hunt animal. This gives the hunter an opportunity to approach closer before he allows the dog to move forward and flush the bird.

Group 8 Retrievers, Flushing Dogs and Water Dogs. These are hunting dogs as well, but their hunting skills are different from those of pointing dogs. They work in the near vicinity of the hunter and flush the birds immediately they find them. Many of the breeds in this group are also excellent retrievers — i.e. will pick up the dead birds and bring them back to the hunter. Their retrieving ability is especially valuable in duck hunting, where the birds often have to be fetched from water. The group includes breeds like the Labrador and Golden retriever, as well as variants of the Spaniel.

Group 9 Companion and Toy Dogs. This is a large and diverse group including breeds like the Poodle, the Lhasa Apso, the Chihuahua, the Pekingese, the Pug and the Boston Terrier. These breeds are companion dogs, and as such they are bred mainly for their easy, amiable nature and special phenotypic appearance. In this group we find dogs with spectacular coats, and breeds with flat noses, rounded skulls and eyes that to some extent mimic those of a child.

Group 10 Sighthounds. Sighthounds are bred for speed and elegance. The majority of the breeds in this group originate from Great Britain or the Middle East. The group includes the Greyhound, the Whippet, the Saluki, the Afghan Hound, the Deerhound and the Irish wolfhound. The dogs were developed originally for hunting, but today their running speed is capitalized upon mainly in dog racing.

Each breed is registered at the international dog society Fédération Cynologique Internationale (FCI) and has a country of origin — an 'owner' country. The owner country writes the international standards and thus defines how the ideal dog should be in respect of various phenotypical features, such as type, health status and behaviour. The standards are applied by judges at dog shows. Denmark is the owner country of five breeds: the Greenland Dog, the Broholmer, the Danish-Swedish Farm Dog (together with Sweden), the Danish Spitz (not yet approved by the FCI) and Old Danish Pointing Dog.
The most popular breeds in Denmark are the Labrador Retriever, the German Shepherd and the Golden retriever.

Breeding Goals

Most Danish puppies are bred in small kennel facilities housing two or three bitches each of which produces one litter per year. Compared with production animals, their selection is much less systematic and primarily performed at the level of the individual dog. Hence, total-merit indices comprising all traits of interest are not available. Instead, to a large extent, it is up to the private breeder to decide which traits should receive most emphasis in selection decisions. However, in all breeds dogs must fulfil certain criteria to be approved as breeding animals. These criteria typically relate to type, health status and/or utility traits. In many breeds within the Danish Kennel Club, dogs must obtain the evaluation 'Good' in an official dog show in order to be approved for breeding. The evaluation is performed by an authorized show judge and focuses on the phenotypic appearance of the dog with respect to movements, quality of fur, and how well the dog's 'type' fits the description set out in the breed standard. In addition, some of the working dogs, sheepdogs and hunting dogs are evaluated for their purpose-specific performance.

Most European kennel clubs were founded in the last few decades of the nineteenth century and are thus more than 100 years old. With the establishment of kennel clubs, and with the more careful recording of stud books, each breed became a closed population, so that crossbreds could not be included in the studbook. As a result of this the breed-specific types became more or less fixed.

Genetic Evaluation and Parameters

As mentioned above, all dog breeds conform to a breed standard which in Europe is described by the FCI. In very general terms dogs can be divided into working dogs and pet/show dogs. While pet/show dogs are bred primarily for their appearance to win conformation shows, working dogs are bred for their ability to perform specific tasks. Herding, hunting and grading are among the more traditional tasks that dogs have been trained and selected to excel in. However, in our modern society dogs are used for a wealth of different tasks — for instance, within certain areas of service to humans such as search, police & rescue, and assistance to blind people. Breeding values are not computed for most traits, and selection is instead based on phenotypic performance. However, breeding values are computed for the most important complex diseases, and specific genetic tests have been and are being developed for monogenetic diseases caused by single mutations.

Genetic Evaluations for Complex Diseases

BLUP animal models are used to generate breeding values free of known environmental effects for the most important complex diseases. Canine hip dysplasia (HD) is a common inherited trait in dogs characterized by hip laxity and disconformity that leads to hip osteoarthritis during maturity and in old age. Diagnoses are based on radiography of the hips. Radiographs are evaluated to give a score for conformation based on the congruency between the femoral heads and acetabulae according to a 5-step scale. Because HD is a complex trait, it is impossible to judge the breeding value of a dog from its phenotype at a high level of accuracy. Therefore, the BLUP animal model is used to evaluate breeding value along the same lines as its use in commercial livestock breeding. As in commercial breeding the most important characteristic in the animal model is that the breeding value of the individual animal is calculated on the basis of phenotypic information from the dog itself and from all related individuals. Based on the registered HD data, a statistical model has been established which, in addition to revealing genetic effect, corrects for sex, age and year of radiography. The heritability is assumed to be 0.25 (estimated in German Shepherds). Breeding values are converted to a relative HD-index taking the outset of the average HD-index for a given breed. The average is set at 100. Thus using dogs with an HD-index >100 will improve the HD status of the breed, whereas using dogs with an HD-index <100 will have a negative impact on the HD status of the breed.

Herniation of the intervertebral disc is another disease in dogs for which genetic evaluations have been established. In hypochondroplastic breeds, the predisposition to intervertebral disc herniation is caused by an early degenerative process which can result in disc calcification [5]. A continuous spectrum of degenerate changes is seen both within and between breeds, suggesting a multifactorial aetiology involving the cumulative effects of multiple genes and environmental factors [6]. The disease most commonly affects Dachshunds [e.g. 7]. Severe disc degeneration with calcification has previously been shown to be highly heritable in this breed, with heritability estimates of 0.47–0.87 [8]. The number of calcified discs at two years of age is found to be a good indicator of the severity of disc degeneration and thus may function as a measure of the risk of intervertebral disc herniation [9].

A breeding programme, based on the association between disc calcification and disc herniation, has been established to limit the incidence of clinical disc herniation in the Dachshund population. All dogs born after 1 January 2006 must undergo a radiographic evaluation before being used for breeding. Their breeding value is calculated using BLUP animal model, assuming heritability of 0.5 and including sex, hair-variant and year of evaluation as fixed explanatory effects. As with HD, breeding values are converted to a relative index. Only dogs with an index above 100 (the average for the breed) can be used for breeding.

Organization and Breeding Programmes

In many countries breeding programmes have been established to minimize the prevalence of specific diseases. In what follows, examples of breeding programmes established by the Danish Kennel Club for some of the Danish dog breeds are described. The examples focus on breeding for improved health and inbreeding control.

Controlling Inbreeding

The closed studbooks, and the many numerically small breeds, make inbreeding control very important, but such control is made more difficult by the relatively flat breeding structure for dogs as compared with some production animals. That is, private breeders play a significant role in mating, and especially in selection decisions. Many breeds are therefore in a situation where they have low genetic diversity and clear signs of inbreeding depression. To address this, the Danish Kennel Club has formulated a set of ‘ethical recommendations’ to breeders, and parts of this document have been adapted by the breeding committee of the FCI. According to the recommendations, inbreeding coefficients of up to 6.25%, equivalent to first cousin matings, are accepted. Intensive use of popular sires is another important factor affecting levels of inbreeding in dog populations. In some breeds a male show winner or champion can be siring the vast majority of all litters for several years leading to a serious decrease in the effective population size and an increase in the risk of inbreeding over subsequent generations. The Danish Kennel Club’s ethical recommendations addresses this issue by stating that no dog should sire more than 25% of the average number of puppies born per year over the course of his entire life. In other words, if a breed registers 200 puppies per year, a dog can sire 50 puppies throughout his entire breeding career. A letter is send to the owner of a male with critically many offspring, and the owner risks being expelled from the kennel club if the male continues to be used.

Breeding Programmes for Monogenic and Complex Diseases

The second highest number of diseases with a genetic basis has been described in dogs. (The highest is in humans.) A total of 507 diseases are listed in Online Medelian Inheritance in Animals (http://omia.angis.org.au/). Of these, 157 are caused by a single locus. Progressive retinal atrophy (PRA)—an inherited eye disease leading to blindness—is a good example of a monogenic disease for which mandatory phenotypic screening programmes have been established in many different breeds. PRA is inherited as an autosomal recessive trait, and the phenotypic screening programme, where clinical diagnosis is made by ophthalmoscopia, cannot identify carriers. However, the molecular basis of PRA has now been identified in many breeds, and therefore carriers can be identified by DNA testing. Presently, the molecular basis of 86 different monogenic diseases is known; the list continues to grow steadily, leading to new opportunities to include DNA diagnostics in breeding programmes. In some breeds potential breeding dogs must be genotyped for specific monogenic genetic diseases, and it is then only dogs that either do not carry the disease allele (one copy) or do not have it in two copies that are used for breeding. In Table 1 the breeds and diseases with mandatory genotyping prior to breeding are listed. It is important to take population size and character into account when advising breeders/breed clubs about how to include a specific DNA diagnostic test in breeding programmes. If the test is going to be performed in a large breed with few affected and carrier individuals, both these genotypes can be excluded from breeding. However, if the test is going to be performed in a small population with a relatively large proportion of affected individuals and carriers, it is advisable to include carriers for breeding for a period of time.

Table 1. DNA tests for monogenetic diseases required in different Danish breeding programmes.

Breed(s)	Disease	Inclusion criteria*
Bedlington Terrier	Copper toxicosis	N + C
Old Danish Pointing Dogs	Myasthenic syndrome	N + C
German Wire-Haired Pointer	Von Willebrand type II	N
Kooikerhondje	Von Willebrand type III	N
Welsh Corgi Cardigan	Progressive Retinal Atrophy (rcd3)	N
Labrador Retriever	Progressive Retinal Atrophy (prcd)	N + C
Poodle, Miniature, Toy and Standard	Progressive Retinal Atrophy (prcd)	N + C
Finnish Lappdog	Progressive Retinal Atrophy (prcd)	N + C
Entlebucher Sennenhund	Progressive Retinal Atrophy (prcd)	N + C
Shapendoes	Progressive Retinal Atrophy (ccdc66)	N + C

*N: Only homozygous normal dogs are approved for breeding; N + C: Both homozygous normal and heterozygous carriers are approved for breeding (the latter only when mated with homozygous normals)

Breeding values are used as selection criteria for some complex disease traits, as described in the previous section. For those breeds and diseases where breeding values are available, it is typically required that breeding animals are better than the population average.

Total-merit indexes are not available, but more than one trait is often considered in selection decisions. For instance, some working dog breeds cannot become conformation champions without having passed adequate breed-specific tests measuring their working abilities. On the other hand, a Border Collie that is a conformation champion in Australia will not necessarily be a good sheepdog, and a Border Collie that becomes a champion at sheepdog trails might not succeed in show rings, because it has nonstandard appearance. Both in respect of conformation shows and trails established to evaluate a specific ability, dogs are scored solely on the basis of an individual phenotypic evaluation.

As a side-effect of the stringent selection within the individual dog breeds and the unfavourable genetic correlations between certain type and health traits, many breeds display a high prevalence of some diseases — including certain cancers, blindness, heart disease, cataract, epilepsy, hip dysplasia and some allergies. Some of these diseases are caused by mutations in single genes, while others are complex traits influenced by both genetic factors and the environment.

Examples of Genetic Trends

Figs. 2 and 3 show the genetic improvement over time for the HD in Golden Retrievers and the calcification-index for Wire-Haired Dachshunds. It is evident that both genetic resistance to HD and calcification have improved over the past decade: the breeding restrictions that have been imposed seem to have had a positive effect.

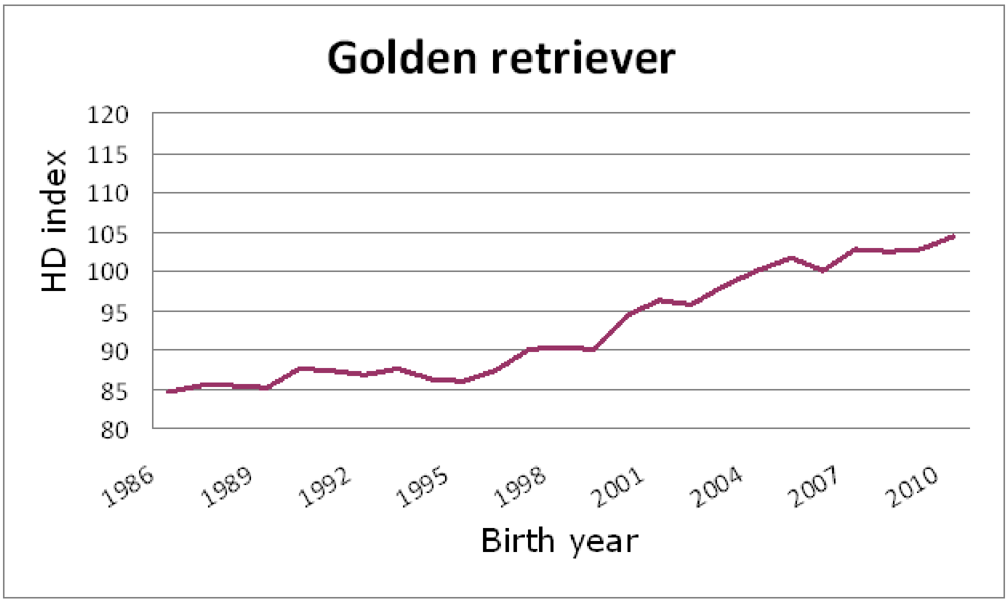

Figure 2. HD index in Golden Retriever 1986–2010 (graph prepared by Kevin Byskov, Knowledge Centre for Agriculture, for the Danish Kennel Club).

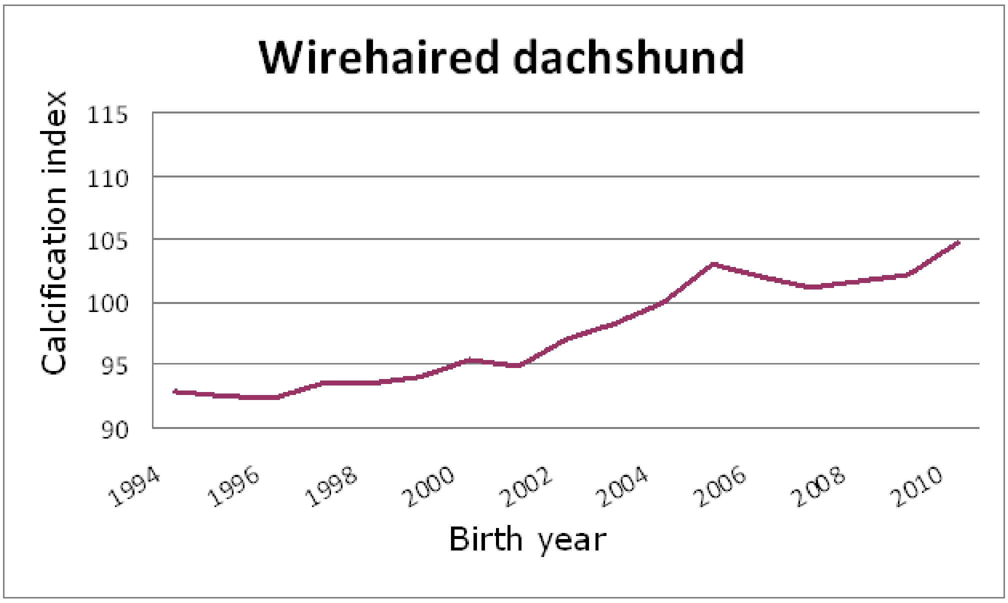

Figure 3. Calcification-index in Wire-Haired Dachshunds 1994–2010 (graph prepared by Kevin Byskov, Knowledge Centre for Agriculture, for the Danish Kennel Club).

Future Perspectives

In recent years the domestic dog has attracted considerable attention as a resource through which the genetics of disease susceptibility, morphology and behaviour can be investigated. This is partly due to the fact that many of the diseases seen in dog populations are analogous to human diseases, and partly due to the unique population structure in dogs. Because dogs show remarkable interbreed homogeneity, coupled with striking interbreed heterogeneity, the dog offers unique opportunities to understand the genetic underpinnings of natural variation in mammals. Genetic studies of dogs are theoretically simpler and more straightforward than those conducted in complex populations, offering many of the statistical conveniences of studies performed in isolated human populations, such as those carried out in Iceland. A disadvantage, as compared with production animals, is, however, the difficulty of accounting for non-genetic factors such as different care regimes, nutrition, and so forth, provided by dog owners, although further advantages are offered by the architecture of the dog genome itself: the dog is known to have longer stretches of linkage disequilibrium, reducing the overall number of markers needed to investigate the whole genome [10]. Taken together, these features suggest that a wealth of new genetic information will be generated in dogs in the years to come. If it is used wisely, this information will greatly benefit dog breeders. However, it may also set up more challenges for those involved in genetic counselling.

References and Further Information

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Further readings:

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The genetics of the dog, edited by A. Ruvinsky and J. Sampson. CABI publishing, UK, 2001

The dog and its genome. Edited by Elaine A. Ostrander, Urs Giger and Kerstin Lindblad-Toh. Cold Spring Harbour, 2007.

Useful homepages:

Databases of inherited diseases in dogs:

http://omia.angis.org.au/
http://www.vet.cam.ac.uk/idid/
http://www.upei.ca/cidd/intro.htm

Kennel Clubs and organizations :

Fédération Cynologique International: http://www.fci.be/
Denmark: http://www.dansk-kennel-klub.dk/Forside (in Danish)
Sweden: http://www.skk.se/
Norway: http://www.nkk.no/
USA: http://www.akc.org/index.cfm
UK: http://www.the-kennel-club.org.uk/

Genetic testing laboratories:

www.optigen.com
www.laboklin.de
www.vetgen.com