Chapter 1.1 The history of animal breeding: science

and application

There are 5 very important aspects that should be considered in animal breeding:

Most importantly, obviously for selective breeding to be successful it is essential that the

trait (e.g. running speed or milk production or coat colour) under selection is heritable.

That animals have different genetic backgrounds so that selection is possible.

The direction of selection is defined by humans and they decide which animals are

allowed to mate and produce members of the next generation.

Success of animal breeding can be judged by looking at a shift in population average

phenotype from one generation to the next. So animal breeding works at population level,

not automatically at individual level.

Success of animal breeding can be measured as the cumulative result of multiple

generations of selection. Breeding decisions are made with the future in mind.

**Definitions**

*A* ***trait*** *is "a distinguishing phenotypic characteristic, typically belonging to an individual". In*

*practice this means anything you can record or measure on an individual.*

*A* ***phenotype*** *is that what you observe or measure on the animal for a certain trait. It can*

*depend both on the genetic background of the animal (provided it is heritable) and external*

*circumstances such as level of nutrition*

**Heritable traits**

Being able to predict the success of animal breeding relies on one very important factor that we

still need to discuss: why does performance in offspring resemble that of the parents? Selective

breeding will only be successful in case the trait under selection is *heritable*. Because only a

fraction of the animals is selected for breeding, so is allowed to produce offspring, and because

the trait is heritable, the performance in the offspring will resemble that of the parents.

Therefore only the best parents are used for breeding and the average of the next generation

will be better than that of the current. A trait is heritable if the performance for that trait, at least

in part, depends on the genetic make-up (DNA) of an animal. Differences in performance

between animals can (partly) be explained by genetic differences between animals. More

details on what this *heritability* involves will follow later in this book. **The scope of this book**

**and this chapter** In summary, animal breeding relates to intentional selection by humans

based on animal performance in a certain environment for predefined and heritable traits. In

most practical animal breeding schemes selection will be on more than one trait

simultaneously. The animals that are superior in this combination of traits will be selected as

breeding animals. In general this combination of traits will consist of traits related to

performance (e.g. milk production, number of eggs, growth, sport performance), health, and

reproduction. The theory behind selection for a combination of traits easily becomes very

complicated. In this book we, therefore, explain the theory behind animal breeding using single

trait selection. In the rest of this chapter we will give you a brief history of animal breeding,

starting from scratch (so from domestication). You will see that developments in animal

breeding have gone hand in hand with developments in society. Then we will look into the

current situation and main challenges. And we will also try to peek into the future: what are the

expected developments in society and how will that influence animal breeding decisions? But

first we will look back at how it all started: with domestication.

Chapter 1.2 Selection by nature

It sounds as if animal breeding is all in the hands of the humans. Compared to natural

populations this indeed is the case, as we decide which animals are allowed offspring and

which are not: selective breeding or in other words *artificial selection*. However, as in natural

populations there is another force that plays an important role and that is the force of *natural*

*selection*. In natural selection it is not us but the environment that determines survival and

reproductive success of animals. So after we have decided which animals we intend as

parents, they still need to be able to survive until reproductive age and to be able to reproduce

successfully. As you can imagine, natural selection also results in directional change in the

population average. Animals *adapt* to their environment and the ones who can do that best will

be the most successful in survival and reproduction. In other words: in natural selection the

direction of selection is on adaptation to the environment.

**Definition**

***Natural selection*** *is the process whereby animals that are better adapted to their*

*environment have a higher change to survive and produce more offspring than less*

*adapted animals. The next generation thus, on average, will be more adapted than the*

*current generation.*

Even though animal breeding is defined as intentional selection by humans, you can see that

natural selection will also play a role. In some cases natural selection will even work in the

opposite direction of selective breeding. In those cases without human intervention the animals

with the desired qualities will be less successful in surviving and/or producing offspring. For

example, the fact that in many cows there is a negative relationship between high milk

production and being able to get pregnant, shows that animals with the desired quality: high

milk production, are less likely to produce offspring unless there is extra effort put into it by the

farmer. Also, the fact that very high producing cows often have health problems indicates that

their chance of producing offspring is reduced compared to their more average producing

'sisters'. Selective breeding often competes with natural selection. We have become so familiar

to the fact that some of the best animals in a breed require assistance with some aspects of

their survivability and/or reproduction that we think it is normal. Domestic animals are 'created'

by humans and to maintain that we accept certain disadvantages. But how far should we go?

For example, some breeds of dogs and beef cattle have been selected such that they are

excessively broad in the head and/or shoulders. But being broad shouldered (or big headed)

creates birth problems. Without human intervention such as assistance at delivery, or even a

caesarean section, both mother and offspring would die. In other words: it is good to keep an

eye on unwanted consequences of selective breeding.

Chapter 1.3 Domestication and animal breeding

Now we will discuss the history of the domestic animals and animal breeding. When did

domestication start, when and how did selective breeding become organised, what is the role of

science in animal breeding, how have animal breeding techniques evolved until now, and what

is the role of society and culture in all this? To start with the first question: how and when did it

all start?

**Definition**

*Domestication is the process of conversion of wild animals to domestic use.*

Domestic animals need to live in (close) association with humans, therefore they have to

become tame. They also have to meet the expectations of their owners for the purpose of

keeping them. This can be achieved by selective breeding. Expectations of owners will change

in time, followed by a change in selective breeding plan. Domestication often has resulted in a

type of animals that has become quite different from their wild counterparts. As a result

domestication often also involves the development of a dependency on humans so that the

animals lose their ability to live in the wild.

**Domestication of the dog**

The first animal species to be domesticated was the dog. Estimates of when this happened

vary a lot, but it was approximately 12,000 years ago. An appealing theory of how this

happened is that when people started to settle down and become farmers, they also started to

accumulate waste. The tamer than average wolves were brave enough to eat from that waste

and thus had a secure source of food. This was an advantage, so natural selection pressure

was on being not very afraid of humans. Eventually, a kind of symbiotic relationship developed,

where these ancestors of the dog started to perform 'tasks' like warning the humans for

approaching danger, helping in hunting, provide warmth, etc. and in return these animals would

receive food security. This type of symbiotic relationship is still present in village dog

populations in Africa and Asia, and also in some Southern European countries. It is believed

that our current domestic dog breeds originate from these village dogs. There is evidence that

genetically the village dogs are in between the wolves and the dogs.

**Domestication of other species**

The symbiotic relationship, such as between human and the ancestors of the dog, most likely is

quite unique for dogs. Other types of animals may have been domesticated more forcefully.

They were captured and put in an enclosure or tied up, at least during the night, and were only

allowed out to graze or scavenge under supervision of a herdsman. Only those animals that

were not aggressive, but also not too shy, managed to adapt to these new circumstances. So

(mainly natural) selective breeding also in these cases was on temperament. In the table you

will find a list of domestic animals with their approximate time and location of domestication.

This is approximate, because especially for ancient times it is difficult to make an accurate

estimate. But even recent events are not always straightforward. Because when do you call an

animal domesticated? And what if it happened in more than one place simultaneously but

independently of each other?

**Table 1.** List of domesticated animals in early times.

Species Latin Date Location

Dog *Canis lupus familiaris* >30,000 BC Eurasia

*Sheep Ovis orientalis aries* 11000 - 9000

BC

Southwest Asia

Pig *Sus scrofa domestica* 9000 BC Near East, China,

Germany

Goat *Capra aegagrus hircus* 8000 BC Iran

Taurine cattle *Bos primigenius Taurus* 8000 BC India, Middle East, North

Africa

Zebu cattle *Bos primigenius indicus* 8000 BC India

*Cat Felis catus* 7500 BC Cyprus and Near East

Chicken *Gallus gallus domesticus* 6000 BC India and South East Asia

Llama *Lama glama* 6000 BC Peru

Guinea pig *Cavia porcellus* 5000 BC Peru

Donkey *Equus africanus asinus* 5000 BC Egypt

Domesticated

duck

*Anas platyrhynchos*

*domesticus*

4000 BC China

Water buffalo *Bubalus bubalis* 4000 BC India, China

Horse *Equus ferus caballus* 4000 BC Eurasian Steppes

Dromedary *Camelus dromedaries* 4000 BC Arabia

Honey bee *Apis* 4000 BC Multiple places

Silkworm *Bombyx mori* 3000 BC China

Reindeer *Rangifer tarandus* 3000 BC Russia

Rock pigeon *Columba livia* 3000 BC Mediterranean Basin

Goose *Anser anser domesticus* 3000 BC Egypt

Bactrian Camel *Camelus bactrianus* 2500 BC Central Asia

Yak *Bos grunniens* 2500 BC Tibet

Asian elephant *Elephas maximus* 2000 BC Indus Valley civilisation

Alpaca *Vicugna pacos* 1500 BC Peru

Ferret *Mustela putorius furo* 1500 BC Europe

Common carp *Cyprinus carpio* Unknown East Asia

Domesticated

turkey

*Meleagris gallopavo* 500 BC Mexico

Goldfish *Carassius auratus auratus* Unknown China

European rabbit *Oryctolagus cuniculus* 600 Europe

Japanese Quail *Coturnix japonica* 1100–1900 Japan

Canary *Serinus canaria domestica* 1600 Canary Islands, Europe

Fancy rat *Rattus norvegicus* 1800s United Kingdom

Fox *Vulpes vulpes* 1800s Europe

European Mink *Mustela lutreola* 1800s Europe

Cockatiel *Nymphicus hollandicus* 1870s Europe

Zebra Finch *Taeniopygia guttata* 1900s Australia

Hamster *Mesocricetus auratus* 1930s United States

Silver Fox *Vulpes vulpes* 1950s Soviet Union

Ball python *Python regius* 1960s Africa

Red Deer *Cervus elaphus* 1970s New Zealand

Atlantic Salmon *Salmo salar* 1969 Norway

Atlantic Cod *Gadus Morhua* On going Norway

Chapter 1.4 Domestication continues

Domestication is not only of ancient times. It is still happening today! It often involves species

that are used for human consumption or for companion, and that become rare in their natural

habitat. To prevent extinction, people try to breed them in captivity. In return benefits are easy

access to the animals, and the possibility to optimise the animals through selective breeding to

the (expected) demands of the market. And 'market' is a very wide concept: demand for food of

animal origin, but also demands of farmers for, for example, dairy cows that can be milked by a

robot, demand for dogs that can perform certain tasks, demand for horses with certain

temperament, etc. There are some (rare) occasions where new tasks are invented for certain

animal species, potentially followed by domestication. A recent example may be that of the use

of 'sniffer wasps' for explosives detection. These wasps are trained to smell different types of

explosives and, subsequently, used in places where it is too dangerous for people (or dogs) to

go to. Because wasps are small and can fly they can go places where robots can't go. Possibly

these wasps in the future will be different from wild wasps. This is due to directional selection

on, for example, trainability.

**Prerequisites for domestication** Domestication is not always successful. Despite many

attempts, the zebra, for example, has not been domesticated. Even though it is closely related

to the horse and the donkey and you can keep it in an enclosed area where it will survive and

reproduce, apart from the exceptional case, it has not been successfully tamed. Several

generations in captivity and some selective breeding did not make the zebra genetically tame

so that it can be ridden. Why is that? People are not sure, but there is a list of prerequisites for

successful domestication that seem to hold. The zebra may not meet one or more of them. The

apparent prerequisites are:

The animals should be able to adapt to the type of feed they are offered by humans. This

may be different (in diversity) from what they were used to in the wild.

Animal must be able to survive and reproduce in the relatively closed quarters of

captivity. Animals that need a very large territory are not suitable to be domesticated.

Animals need to be naturally calm. Very skittish or flighty animals will be hard to prevent

escaping.

Animals need to be willing to recognise humans as their superior, which means they

must have a flexible social hierarchy.

Animal species that do not meet all the above criteria will be very difficult to domesticate. But a

fair number of animal species have been domesticated, and the number is still increasing. The

early domestication probably was mainly driven by natural selection: the animals that managed

best were most successful in producing the next generation. Real selective breeding is of fairly

recent origin.

Chapter 1.5 Origin of animal breeding: a history of

science

**The start in the 18-th century**

Until roughly the 1700's animal breeding, as in selective breeding, did not really exist. Of course

people mated their animals with animals in the neighbourhood that they liked. There was no

*systematic way* of selecting animals for reproduction, based on *predefined characteristics* that

did not change from mating to mating, but remained similar in time. In Europe, the origin of

animal breeding lays in the United Kingdom. It was Sir Robert Bakewell (1725 – 1795) who

introduced keeping accurate records of performance of animals so that objective selection

became possible. He used inbreeding (mating of related animals with similar traits) to fix certain

characteristics in animals and he also introduced *progeny testing*: the method of evaluating

performance of the first (small) group of progeny and use that information to select the best

father of future progeny. He promoted the idea to 'breed the best to the best'. Bakewell

developed the New Leicester sheep from the old Lincolnshire breed. The New Leicester had

good quality fleece and a good fatty shoulder that was popular at the time. Bakewell also

noticed that Longhorn cattle were growing well and used less feed compared to other cattle. So

he developed that further in order to grow more meat efficiently. It is amazing he did this

without knowing anything about genetics.

**Establishment of herdbooks**

With time the number of people increased who were using the selective breeding approach

introduced by Bakewell. With the growing number of generations of selective breeding, it

became increasingly difficult to remember the relationships between the animals, especially

further back in the pedigree. This was the reason to start recording pedigree on paper, so that

correct information could be reproduced and it could be proven that an animal was of a certain

breed. The first herdbook was for the thoroughbred horse and was established in England in

1791. This book did not contain all pedigree, but only those of horses that were winning

important races. Following the race horses, the Shorthorn cattle (1822) were next to start a

herdbook. In the rest of Europe, herdbooks only started to be established in from 1826 onwards

for horses (in France), and from 1855 onwards for cattle (also in France). The first international

herdbook was established for the American Berkshire pigs in 1876. The first dog in the

Netherlands was registered by the Koningklijke Nederlandsche Jachtvereeninging Nimrod

(predecessor of the Raad van Beheer op Kynologisch Gebied in Nederland) in 1874. After the

turn of the century animal breeding within herdbook settings became standard.

**Creation of breeds**

With the establishments of herdbooks, breeds were formed. There is still debate on what is a

true definition of the term 'breed'. This is nicely illustrated in dog breeding by the fact that the

Fédération Cynologique Internationale (FCI), the international federation of kennelclubs, which

are national organisations across herdbooks, recognises 339 separate breeds, while the

English Kennelclub recognises 210 breeds, and the American Kennelclub even only 162.

**Definitions**

*A* ***breed*** *is a group of animals of a certain species that through generations of selective*

*breeding has become uniform in performance, appearance, and selection history*

*A* ***species*** *is the largest group of animals that are capable of interbreeding and producing*

*fertile offspring*

It is interesting to realise that these herdbooks were established without any knowledge about

genetics. Breeders had a feeling about inheritance and that was sufficient to invent this

selective breeding.

Chapter 1.6 Breeding in the 19-th century

In 1859, Charles Darwin (1809 – 1882) published his book 'On the origin of species', based on

the findings that he collected during his voyage on 'the Beagle'. He discovered the forces of

natural selection. He also concluded that the individuals that fit best in their environment have

the highest chance to survive and reproduce: they are the fittest. Consequently, different

environments result in different directions of selection pressure. He based this on his findings

on the Galapagos islands, where finches on one island were different from finches on the next

island. His conclusion was that the difference in food source, predators present, etc. between

the islands had made the finches develop differently over very many generations. They

adapted to their specific environments.

Darwin translated his ideas to domesticated species as well: ***"We cannot suppose that all the***

***breeds were suddenly produced as perfect and as useful as we see now them; indeed, in***

***several cases, we know that this has not been their history. The key is man's power of***

***accumulative selection: nature gives successive variations; man adds them up in certain***

***directions useful to him. In this sense he may be said to make for himself useful breeds"***

C. Darwin. On the Origin of species (1859, p.30)

Still, Darwin did not know about the basic laws of inheritance. It was the monk Gregor Mendel,

who in 1865 published the results of his studies of genetic inheritance in garden peas. He

showed that genetic material is inherited from both parents, independently of each other. And

that each (diploid) individual thus carries 2 copies of the same gene, of which only 1 is passed

on to their offspring. Which one is a result of chance (*independent assortment)*. He also

showed that these gene copies (alleles) can be dominant (only 1 copy determines the

expression of the gene), recessive (2 copies are required for expression), or additive (a copy of

both alleles result in an expression that is intermediate to that of having 2 copies of either of the

alleles). These findings had no immediate impact on animal breeding and were not recognised

as important until 1900.

Chapter 1.7 Animal breeding in the 20-th century

Most of the animal breeding theory we are still using today, was invented in the first half of the

20-th century. The statistician R. A. Fisher (1890 – 1962) showed that the diversity of

expression of a trait could depend on the involvement of a large number of so-called Mendelian

factors (genes). He published a lot related to statistics and animal breeding, but his keynote

paper came out in 1918. Fisher, together with Sewall Wright (1889 – 1988) and J.B.S. Haldane,

were the founders of theoretical population genetics. Thomas Hunt Morgan (1866-1945) and coworkers

connected the chromosome theory of inheritance to the work by Mendel and created a

theory where chromosomes of cells were believed to carry the actual hereditary material.

Morgan won the Nobel prize for it in 1933.In the first half of the 20th century Iowa State

University in Ames, Iowa, USA was the place to be. It was home to Jay L. Lush (1896 – 1982),

who is known as the modern father of animal breeding. He advocated that instead of subjective

appearance, animal breeding should be based on a combination of quantitative statistics and

genetic information. His book 'Animal Breeding Plans' that was published in 1937 greatly

influenced animal breeding around the world. Lanoy Nelson Hazel (1911-1992) was inspired by

Lush's book and started working for him, also in Ames. He received his PhD degree in 1941

and in that PhD thesis he developed the selection index theory, a method used for decades to

determine what weights should be put on the different traits under selection. In the process of

developing this method he also came up with a concept on how to estimate genetic

correlations. This is essential for assigning the proper weight to selection traits. Hazel also

developed a method using least squares, a statistical technique, for more complicated data with

unequal numbers of subclasses as often occur in animal data. Until then, statistical techniques

by Hazel were used to optimise weighing the performances for various traits in animals to

select those with the most optimal combination. The estimated breeding value (ebv) was only

developed later by the statistician C. R. Henderson (1911 – 1989), who was a student of Hazel

in Ames. The estimated breeding value made it possible to rank the animals according to their

estimated genetic potential (the ebv), which resulted in more accurate selection results and

thus a faster genetic improvement across generations. Henderson further improved the

accuracy of the estimated breeding value by deriving the best linear unbiased prediction

(BLUP) of the ebv in 1950, but the term was only used since 1960. He also suggested to

integrate the full pedigree of the population to include genetic relationships between individuals.

This way performance of relatives could be included in estimating the breeding value of an

individual. The so-called animal model was born. Unfortunately in those days the computer

power was too limited to be able to also calculate the breeding values using the animal model.

The practical implementation thus had to wait until the later 1980's. Current great minds that

have developed a way to incorporate large scale DNA information that has become available in

animal model (BLUP) theory to estimate the so-called genomic breeding values are Theo

Meuwissen (currently professor in Ås, Norway) and Mike Goddard (currently professor in

Melbourne, Australia).