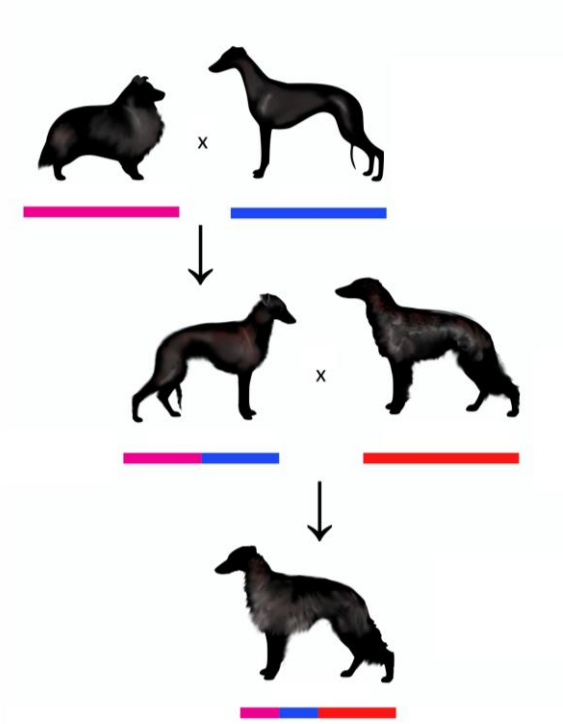

BREEDING STRATEGIES WITH OUTCROSS

There is not a lot of knowledge about outcross in the world of dog breeding. It's time to change that, because dog breeders are increasingly confronted with situations in which they are no longer able to make responsible breeding choices within their chosen breed. This document will go over different ways to incorporate outcross in a breeding program.

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Breeding strategies with outcross

Purebreds and crossbreds

Outcross, or purposeful crossbreeding, is like sacrilege in the purebred dog fancy. It hasn't always been that way. Breed purity and closed studbooks are relatively new as a concept. Historically, dog breeds were regularly crossbred. Today, a large portion of animal breeding still considers crossbreeding as a normal breeding practice: the livestock breeding industry. Crossbreeding of livestock breeds is an accepted practice, because people know: crossbreeds serve a purpose.

That sounds incredible to a lot of purebred dog breeders, because what is a breed if there is no breed purity? The answer to that question depends on how you define a breed. What is a breed? There are multiple answers to that question, depending on who you ask, and you could write a whole piece about it (perhaps another time!). For now, this will be the definition: A breed is a group of animals that possess certain traits because of selective breeding. Variations on this definition are used by agricultural organizations, biology books, and dictionaries. Curiously, breed purity is not part of the definition of what makes a breed, whether you ask the FAO (Food and Agriculture Organization of the United Nations), Biology Online (the largest online biology database in the world), or social scientists ("a breed is a breed when people say it is").

A breed is a group of animals that possess certain traits because of selective breeding. In other words: a breed is about traits. Breeders select for traits, which is how they create or maintain breeds. The essence of a breed is in the traits, not in rigid breed purity.

The Eurasier is a dog breed. Right? Most people will undoubtedly answer 'yes', because this breed is recognized by the FCI. At least, it is now. If you had asked this question to dog fanciers in 1960, they would undoubtedly have answered 'no'. That is because 1960 was the year when a Chow Chow was bred to a Keeshond, which would eventually lead to the breed we know today.

Examples from the livestock breeding industry

A breeder has lots of options when it comes to selection—in other words: breeding! The first breeding method that comes to mind is breeding within the breed. But like I mentioned before: crossbreds serve a purpose. There are a myriad of reasons why a breeder might choose to venture out of their chosen breed. It all depends on the breeding goal: what does the breeder want to achieve? We know a lot about reasons to crossbreed from the livestock breeding industry:

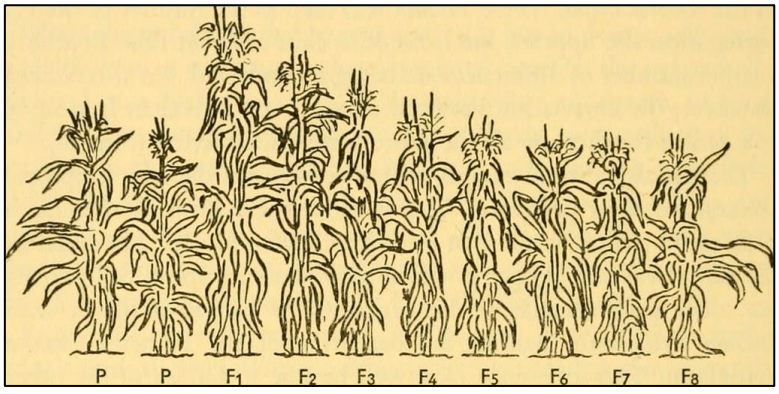
- **Heterosis**

  Heterosis is another word for a phrase that is infamous in the purebred dog fancy and that many breeders choose not to believe in: “hybrid vigor”. It is important to realize that heterosis really exists, but it doesn’t work the way you would expect. Heterosis means that a crossbred possesses better traits than its purebred parents. These traits have mostly to do with fertility, vitality, and health (litter size, life expectancy, immune system, etc.) These are traits that are notoriously hard to breed for using only selection, because they have a low heritability.

  It is unclear how heterosis works, exactly, so it is difficult to explain. But heterosis is easily observed, which is why it is abundantly and enthusiastically used in horticulture and livestock breeding. Research on heterosis in dairy cattle, published in 2008, indicates heterosis of 10% for fertility and 10-15% for life expectancy. Dairy cow crossbreds were 10% more fertile and lived 10-15% longer than the original purebred breeds.

  So, heterosis has a positive effect on fertility, vitality, and health. But heterosis is not heritable, which means it is not a trait you can select for. Heterosis is a temporary effect. This effect lessens with each consecutive generation without further crossbreeding, and will eventually disappear.

  We differentiate between various kinds of heterosis: individual heterosis, maternal, and paternal heterosis. Individual heterosis is the heterosis within an individual. These are the positive effects that an animal will experience because it is a crossbred itself. Maternal and paternal heterosis are the positive effects that are caused because the mother or father is a crossbred. For example, the father to have better sperm quality and get more offspring, and the mother might have offspring with a higher body weight after weaning.



Heterosis observed in plants, as illustrated in the book ‘Elements of Genetics’ in 1950, written by C.D. Darlington and K. Mather. Two different inbred lines (P) are crossed. It creates the first generation F1, the second generation F2, etcetera. The first generation shows a tremendous heterosis effect. With every consecutive generation the effect lessens, until there is no difference compared to the original lines.

- **Combining traits**
  It is difficult to select a breeding line for multiple traits at the same time. It makes a lot more sense to specialize a breeding line. This is what happens in the livestock breeding industry, like pig breeding. For example, in pigs, two breeding lines could be crossed where one is specialized in large litters (but less growth) and the other is specialized in growth (but smaller litters). By combining these lines, you'll get pigs with relatively large litters that grow relatively fast.

- **Improving traits**
  Sometimes breeding for multiple traits isn't only difficult, it is impossible. Another example from the pig breeding industry: the traits for lean meat and meat quality. These two traits are negatively correlated, which means you cannot breed for both traits at the same time. If you want a pig with a lot of lean meat but also good quality meat, you can only get that in a crossbred pig.

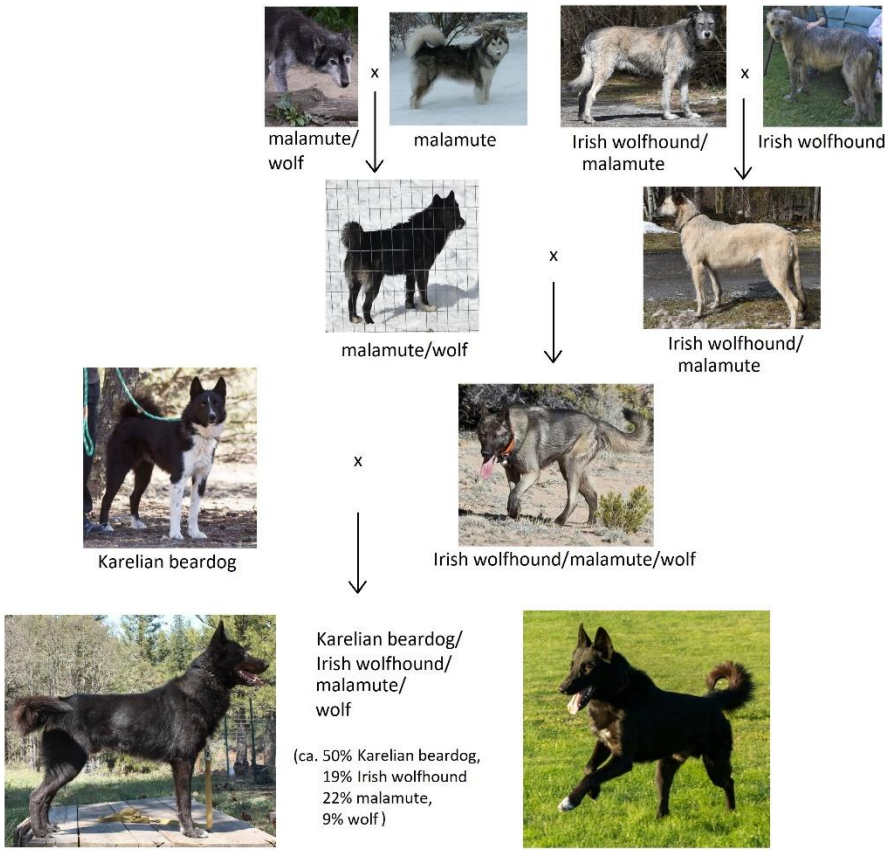
- **Protection of breeding lines**
  This reason lies squarely outside the realm of dog breeders, but it is interesting to see what breeding can be like in other animal species. Certain pig breeders invest a lot of time and money into developing specialized breeding lines. These pigs have such perfected traits, that their breeders will do anything to prevent their valuable genetics falling into the hands of other breeders who might profit from them. That's why these breeders will only ever sell crossbred pigs from their perfected breeding lines. This way, the offspring will experience the positive effects of heterosis and the combining of traits (growth, mother instinct, meat quality, etc.), and at the same time the breeding lines are protected.

By now it should be clear that crossbreeding is very normalized in the livestock breeding industry, because the breeding goal and the desired traits are key. These are important lessons for dog breeders. Crossbreeding is nothing to be scared of, and it can be very useful.

These are uncertain times for the purebred dog fancy. More and more research is published that indicates it is necessary to open up the studbooks. For the Netherlands in specific, there are Dutch welfare criteria that all dogs should meet, new procedures for extreme short-nosed breeds… One thing is for sure: we live in a time of change. Times are especially uncertain for breeders of 12 extreme brachycephalic breeds (affenpinscher, boston terrier, English and French bulldog, the three Belgian griffons, Japanese spaniel, King Charles spaniel, pug, Pekingese, and shih tzu). In these breeds, hardly any dog meets the Dutch welfare criteria, or even no dog at all. The Dutch minister of in charge of these criteria makes only one exception that allows breeding with dogs that do not meet the welfare criteria, and that is by breeding them to dogs that do meet the criteria. In other words: crossbreeding.

For most breeders this will feel like jumping in the deep end. Thankfully, lots of knowledge is readily available from the livestock breeding industry. Supported with that knowledge, we venture out.

So what kind of methods of crossbreeding are out there?



An example how breeding choices are shaped by the breeding goal. At first glance, the above pedigree might consist of a bunch of random dogs. This would be a wrong assumption, because every combination is thoughtfully made by the respective breeders with their breeding goal in mind. In the upper right are dogs from an Irish wolfhound/malamute breeding program aimed at breeding healthy dogs in the spirit of the Irish wolfhound. You can read more about them further ahead in this document. Down in the pedigree you see a program aimed at breeding working dogs. The breeding goal: healthy, large, hardy, versatile hunting and companion dogs for the backcountry, predator aggressive, sticky, clean, and no excessive barking. The Karelian beardog is a fierce, medium sized, guardian and predator hunting dog prone to barking. It was mated to a large, hardy, quiet, friendly descendent of Irish wolfhound, malamute and wolf, in order to preserve the hunting instinct, lessen barking, and add size. An estimation of ancestral percentages is shown above. A DNA test of an offspring (below) shows how the true percentages can deviate from the estimates. This individual did not inherit any traceable genes from its wolf ancestors.

Breeding strategies

There are many ways to incorporate outcross in a breeding program. Which way is most appropriate depends on the breeding goal. What do you want to achieve? It's important to take a moment to determine this clearly. For short-nosed breeds, the breeding goal might consist of preserving temperament traits and breed type, while also complying to the Dutch welfare criteria. In other words, it is imperative to determine the essence of a breed. Which traits truly make the breed? These traits determine the breeding goal together with the welfare criteria.

Next, determine where you are going to get your desired traits. Which dogs outside of your breed have the traits that you want to incorporate? The choices you make here, determine the breeding strategy. I will now go over several breeding methods, illustrated with examples from the livestock breeding industry, but also with some examples of canines!

Cross of 2 breeds

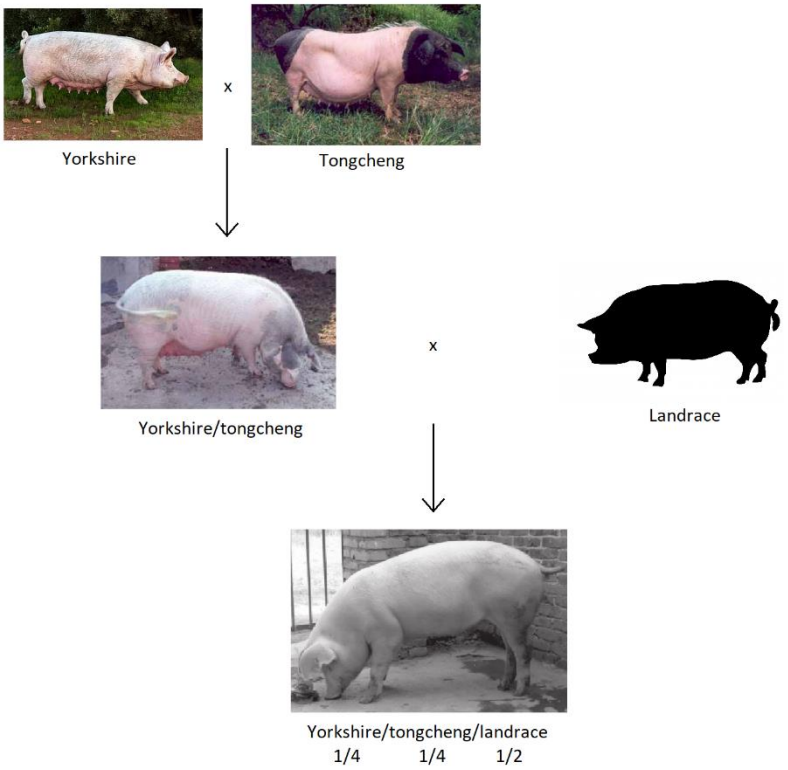
The simplest type of cross is a cross between two breeds. Breed A is crossed with breed B and then you get the offspring F1 (generation 1) that inherited 50% of its genes from parent A and 50% from parent B. This cross is used a lot in sheep and dairy cattle. Most of the time, the F1 is not used for breeding as it only serves for production, due to reasons mentioned above in 'examples from the livestock breeding industry'. When a cross is done purely for production and the offspring isn't bred from, it is often referred to as a 'terminal cross'. A cross between two breeds experiences optimal individual heterosis, especially when both breeds are genetically very distinct.

P (parent)	A x B
F1 (first generation)	AB

Cross of 3 breeds

A cross between three breeds is slightly more complicated. Breed A is crossed with breed B, which gives offspring AB who is crossed with breed C, and you end up with offspring ABC. This offspring has inherited 50% of its genes from parent C and about 25% of its genes from parents A and B. When you do this cross, you can profit from the maternal heterosis in the F1 (AB) parent, because heterosis causes better fertility. Also, the offspring ABC experiences optimal individual heterosis.

P (parent)	A x B
F1 (first generation)	AB x C
F2 (second generation)	ABC

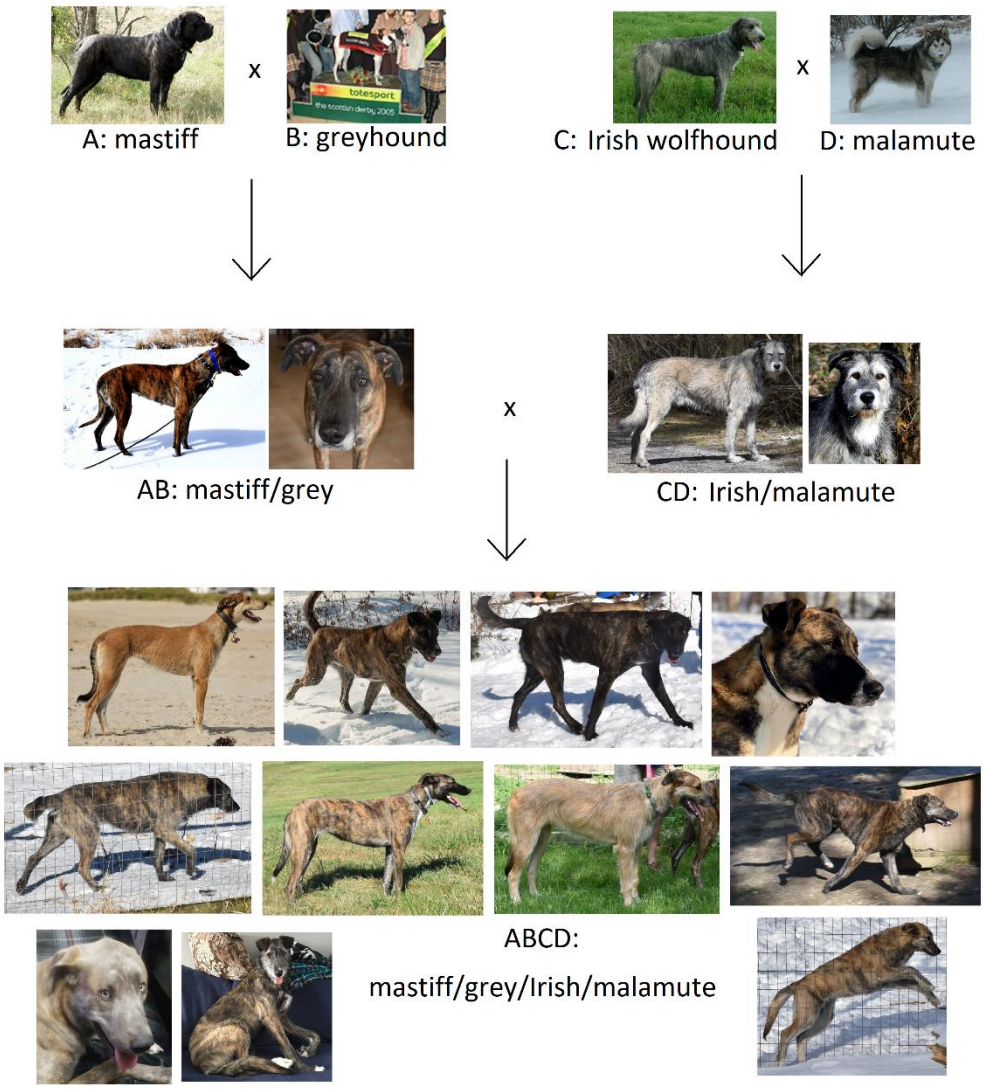


Here you see a cross between three pig breeds, that is done for research aimed at the preservation of the Chinese Tongcheng pig. They are searching for reasons to get farmers interested in using Tongchengs. The Tongcheng pig is known for great maternal instincts. To utilize this trait, a Tongcheng sow was mated to a Yorkshire boar (picture above is of a sow). Yorkshire pigs are known for great meat quality. The F1 is a pig with good maternal instincts and good meat quality, which was crossed with the landrace pigs that are kept by local farmers. The F2 is a pig that experiences optimal heterosis, and that thrives with the low nutritional feed of local farmers.

Cross of 4 breeds

In a cross of four breeds, breed A is crossed with breed B to produce offspring AB, and breed C is crossed with breed D to produce offspring CD. Then animals AB and CD are crossed together to produce offspring ABCD. This cross has inherited approximately 25% of its genes from parents A, B, C, and D. A cross between four breeds makes optimal use of both maternal and paternal heterosis by using two different F1 parents (AB and CD). This cross is often done in chicken breeding to make use of all types of heterosis, to improve traits and to combine traits. When crossing four specialized breeds, these chicken breeders hit three birds with one stone.

P (parent)	A x B		C x D
F1 (first generation)	AB	x	CD
F2 (second generation)		ABCD	



An example of a cross of four breeds in dogs. A mastiff (A) x greyhound (B) x Irish wolfhound (C) x Alaskan malamute (D). Both crosses AB and CD were done to improve breed A and breed C, respectively. Both breeding programs are discussed later in this document. The purpose of this cross of four breeds is to breed giant but healthy dogs that live to an old age. A friendly but brave and athletic dog that has a good maintenance free coat suitable for the cold weather in the American state Vermont. The mastiff/grey (AB) has a thin coat that is unsuited to cold climates, and the Irish/malamute (CD) has a thick coat that needs maintenance. All ABCD offspring have a maintenance free coat that is suitable for cold climates. Traits of all four breeds are represented in the offspring, though some pups tend more towards one ancestor. The AB litter consisted of 9 pups, the CD litter of 5 pups, and the ABCD litter consisted of 18 puppies. Heterosis? This is a sample size of only one litter, so you cannot say for sure that the large number of pups is due to heterosis effect. To get more insight, you would have to repeat similar breedings to get a larger sample size and therefore more data.

The breeding strategies mentioned up to this point are mostly done as terminal crosses in the livestock breeding industry, which means the final offspring is not bred from. The following strategies are aimed at the long term. In other words, the crossbred offspring is used to keep breeding new stock.

Rotation of 2 breeds (crisscross, two way rotational)

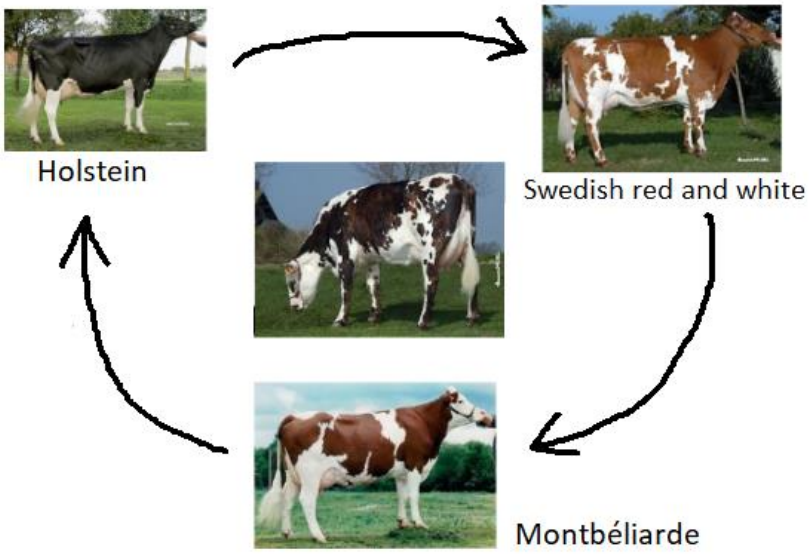
In a rotational cross between two breeds, breed A is crossed with breed B to create offspring AB. This offspring is bred to breed A, those offspring are bred to breed B, those offspring are bred to breed A again, and so on. A condition for this breeding strategy is that both breeds A and B continue to be bred in purebred lines, which means a rotational breeder depends on purebred breeders. After several generations, an equilibrium is reached in the percentage of genes from the parent breeds that are present in the offspring: it stabilizes at 35% and 65%, where 65% of the genes come from the most recently used breed. Heterosis stabilizes as well at approximately 67% of the heterosis you would get when breeding a cross of two breeds.

P (parent)	A x B
F1 (first generation)	AB x A
F2 (second generation)	AB x B
etc	etc

Rotation of 3 breeds (crisscross, three way rotational)

A rotational cross between three breeds works roughly the same as a rotational of two breeds. Breed A is crossed with breed B, getting offspring AB. This offspring is crossed to breed C, with offspring ABC. Then this offspring is bred to breed A, those offspring to breed B, those offspring to breed C, those offspring to breed A again, and so on. Heterosis stabilizes at approximately 85%. Three way rotationals in dairy cows are known to produce cattle with high scores on fertility, claw and udder health, and calf vitality. The crossbred animals are quite homogeneous: they have a comparable temperament and phenotype, despite being comprised of three breeds.

P (parent)	A x B
F1 (first generation)	AB x C
F2 (second generation)	ABC x A
etc	ABC x B
	etc

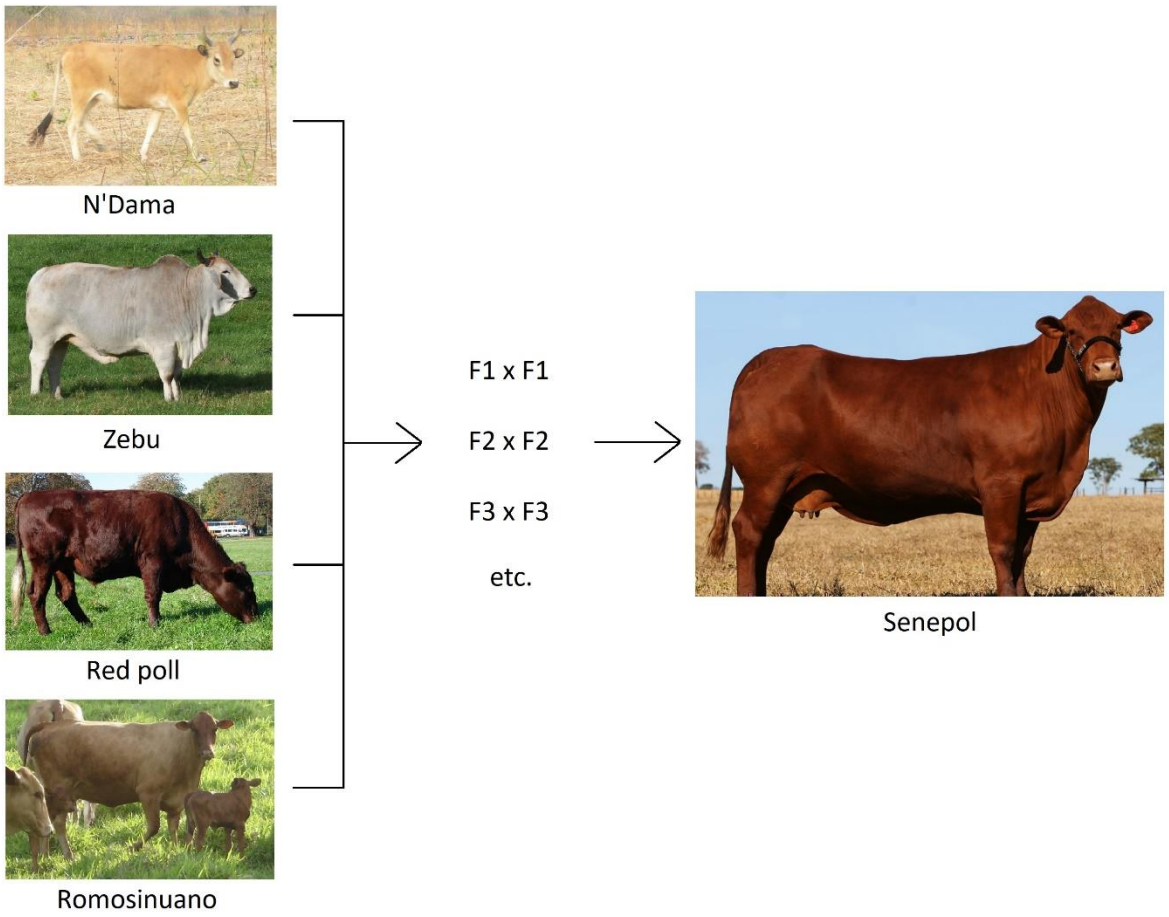


Dairy cow crossbreeding is all about health, life expectancy, the contents in milk (like protein content), and residual value (total worth of the cow after production). Two way and three way rotationals outshine purebreds in for example udder health and fertility. When it comes to milk production, the Holstein is superior, which is why this breed is the most common dairy cow in the world. However, the Holstein is also the breed with the lowest fertility, high inbreeding levels, and a fragile constitution. That is why about 2000 dairy farmers in the Netherlands choose to own crossbred dairy cattle. This is an example of a three way rotational with Holstein, Swedish red and white, and Montbéliarde, with an offspring in the center.

Synthetic breed

Unlike breeders of rotationals, a breeder will no longer depend on purebred stock when choosing for a synthetic. In a synth, breed A is crossed with breed B, which creates the F1 offspring AB. From there on, F1 animals are bred to other F1 to create the second generation, the F2. The F2 is also bred with F2 to create the F3, which is bred to F3 to create the F4, and so on. In theory approximately 50% of breeds A and B remain present in the population. A synthetic can be created from multiple breeds, but the principle remains the same. The F1 is bred to F1, the F2 to F2, etcetera. The Flevolander is an example of a synthetic sheep breed. The breed was created from the Finnsheep and the French Ile de France. The Finnsheep is known for its beautiful coat and fertility, while the Ile the France is known for its meat quality and a long rut. The resulting synthetic breed is the Flevolander, a vital breed with a beautiful coat, and females lamb without complications up to three times a year, often with twins.

P (parent)	A x B		A x B
F1 (first generation)	F1 AB	x	F1 AB
F2 (second generation)	F2 AB	x	F2 AB
etc		etc	



The synthetic breed Senepol was created in the Caribean for the need of allround cattle that could handle the climate. The Senepol was created from four breeds: N'Dama, Zebu, Red poll, and Romosinuano. The African N'Dama and Zebu cattle are able to handle high temperatures, the European Red poll was used to increase milk production and get rid of horns, and the Colombian Romosinuano was used for its docile temperament and meat quality.

Introgression: backcross and the 'droplet method'

Introgression means that new genes are added to an existing breed. Several Dutch dog breed clubs are already carrying out an outcross program utilizing the so called 'droplet method'. This method of outcrossing is now fairly well established in the dog fancy, because it is the only breeding strategy out of all those mentioned in this document that is relatively well accepted.

When doing introgression, a single cross is done between breed A and breed B, resulting in offspring AB. This offspring is then crossed to breed A, and so is the offspring in the F2, F3, and so on. This type of crossbreeding is also called backcrossing, because after the initial cross the offspring is crossed back to the first breed. Breed type of breed A returns very quickly, which is the reason why this kind of outcross is reasonably well accepted by purebred dog breeders. Within three generations, the offspring will possess the breed traits of breed A again, by then having inherited approximately 85,5% of the genes of breed A. The downside of this is that new (and wanted) traits also disappear very quickly.

The droplet method is based on backcross. Once in every few litters, a cross is done and the offspring is slowly bred back into the breed. Examples of breed clubs who are currently doing outcross projects with the droplet method are the Dutch breed club for Saarloos wolfdogs AVLS and the Dutch breed club for

Wetterhouns NVSW. They are seeking to add as much genetic diversity as possible, without sacrificing breed type in the overall breed. If you want to increase genetic diversity in a breed, the droplet method is not the most efficient way of going about it. By backcrossing every generation, you quickly lose much of the newly gained genetic diversity. But it has to be said that getting outcross projects approved at all was a momentous achievement for these clubs, and the most important reason these projects were approved by the club members was the promise of a quick return to breed type. Garnering national and international attention for outcross is another important achievement, and people have slowly gotten more used to the concept. The projects are now several generations underway and people can see the offspring with their own eyes. People are gaining confidence, and are starting their own outcross endeavors.

Introgressions works best when the added trait is inherited dominantly, or if there is a genetic marker for the trait. An example is the booroola gene that was bred into the Texel sheep using a backcross with a Merino sheep. The booroola gene causes sheep to get more offspring, but the Texel sheep did not possess this gene. The Merino sheep does, so the Merino sheep donated the booroola gene to the Texel sheep. All backcross Texel sheep now get twice as many offspring as the other Texels. A more well known example in the dog world is the LUA Dalmatian. In the '70s an English pointer named "*Shandown's Rapid Transit*" was crossed into the breed to introduce the gene for normal uric acid. Offspring of this single cross were crossed back to Dalmatians. All offspring that inherited the gene for normal uric acid are called LUA (low uric acid).

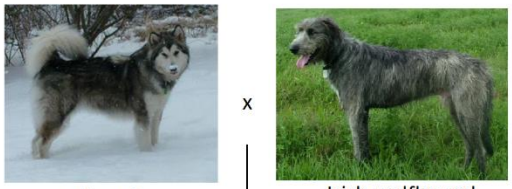
P (parent)	A x B
F1 (first generation)	AB x A
F2 (second generation)	AB x A
etc	etc

1973
"Stocklore Hybrid"

1980
"Stocklore Stipples"

1982
"Blackeyed Susan"

To the left you see the F1 "Stocklore Hybrid", daughter of the English pointer "Shandown's Rapid Transit" and Dalmatian bitch "Lady Godiva". "Stocklore Hybrid" inherited the gene for normal (low) uric acid from her pointer sire. The gene is a simple dominant, which means it was easily bred into the Dalmatian utilizing backcross. Dalmatians with breed typical spots were bred within three generations, like "Stocklore Stipples" and her daughter "Blackeyed Susan". LUA Dalmatians are very popular and well known these days, and are owned by people who love the breed but who do not love the painful disease.


malamute

x

Irish wolfhound


F1: Irish/malamute
1/2 1/2
(50% Irish wolfhound)

x


Irish wolfhound

F2: Irish/malamute
3/4 1/4
(ca. 75% Irish wolfhound)

An example of how quickly breed type returns after a single backcross. A mate was sought that was genetically distinct from the Irish wolfhound, a dog known for its good health, with a powerful but athletic body without exaggerations, and that would be able to handle the cold climate of the American state Vermont. The choice fell on an Alaskan malamute. The F1 litter consisted of five puppies that grew to be large and strong dogs with a rough, thick coat. An F1 male was bred to a purebred Irish wolfhound in a backcross, which resulted in an F2 litter of eight pups. The litter was very homogeneous and saw a major return to Irish wolfhound breed type (see F2, right). A repeat litter resulted in another eight pups, again full of breed typical Irish wolfhound puppies, with the exception of one puppy whose appearance deviated a bit (see F2, left). This puppy reminds a bit of old photos of Irish wolfhounds back when the breed was being restored in the 19th century. Below you see "Cheevra", one of the ancestors of the modern Irish wolfhound. "Cheevra" herself was a mix of Great Dane and Deerhound. She had an incorrect coat that was 'too flat', a trait that was corrected in following generations.

Boxer x Welsh corgi Pembroke

F1: boxer/corgi
1/2 1/2
(50% boxer)

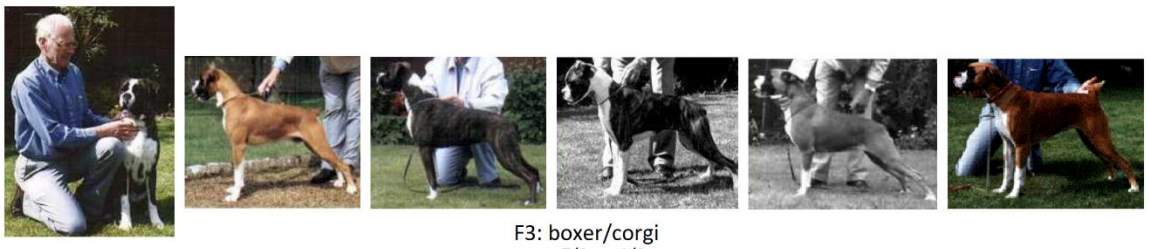
x

Boxer

F2: boxer/corgi
3/4 1/4
(ca. 75% boxer)

x

Boxer



F3: boxer/corgi
7/8 1/8
(ca. 87,5% boxer)

F4: boxer/corgi
15/16 1/16
(ca. 93,8% boxer)

F5: boxer/corgi
31/32 1/32
(ca. 96,9% boxer)

Above are five generations of Bruce Cattanach's boxer x corgi outcross project. As a geneticist and boxer fancier, he wanted to know if he could introduce the bobtail gene into the breed by doing a crossbreeding with a corgi. At this point in time (the '90s) countries started to introduce docking bans, so the idea of a boxer with a naturally short tail was an appealing one. Adjusting breeding strategies is a natural result when facing changing laws and regulations. The F1 was very homogeneous, all pups had short legs and some did indeed have a bobtail. Every following generation was backcrossed. Some pups in the F2 still had short legs, but others saw a dramatic return to boxer breed type. From the F3 onwards all offspring were recognizable as boxers.

mastiff

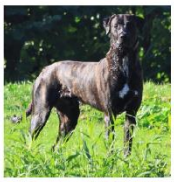
x

racing greyhound

example

mastiff

x



F1: mastiff/ racing greyhound

1/2 1/2

(50% mastiff)

x

mastiff

a. F2: mastiff/racing greyhound

3/4 1/4

(ca. 75% mastiff)

b. F2: mastiff/racing greyhound

3/4 1/4

(ca. 75% mastiff)

male

female

F2 sire

(F1)

F2 female

F2 dam

(purebred)

F2 male

(continuation of previous page)

Here you can see the offspring of a cross between an English mastiff and a racing greyhound, that was done to improve the health of the mastiff and to increase genetic diversity. The mastiff is a breed that has high levels of inbreeding, which results in problems like infertility. The breed's average life expectancy is very low, and the breed also suffers from health problems like joint issues, eye issues and skin issues. The dog used for outcross was a powerful dog full of vitality that lived to an old age: a racing greyhound.

The F1 litter consisted of nine pups that looked like 'greyhounds on steroids' as adults. The F1 adults are social and curious, friendly, intelligent and easy to train. They aren't guardians, but they make good watchdogs. Multiple backcross litters were born. F2 litter a. consists of a singlet and F2 litter b. consists of nine puppies. Contrary to the F1, the F2 dogs are very divergent in type. Some pups tend towards the racing greyhound type, and others show a clear return to mastiff breed type which shows in a coarser head and body. It is interesting to note that the b. litter has a clear distribution, where the bitches have the slighter build of their F1 sire, and the dogs have the coarser build of their mastiff mother.

Possibilities

There are many ways in which outcross can be incorporated in breeding programs. The breeding strategy that fits best, depends on your breeding goal. You don't necessarily have to choose one single strategy, you can also choose to combine strategies. For example, if you want to add a specific trait to a breed and that trait is highly heritable and therefore easily selected for, a single backcross might be a good idea. If you seek to add lots of genetic variation to a breed, a single backcross won't be very useful to your program. Instead, it might be a better idea to embark on a large crossbreeding program, utilizing multiple outcrosses using different breeds. Offspring could be bred back into the breed using backcross, but also to each other using synthesis. You could keep different breeding lines within the breed, with some breeders focusing on the backcross lines and others focusing on maintaining synths. The backcross lines will soon be breed typical again, and the synths can be used for rotational crosses. This way, genetic diversity can also be maintained in the long term.

These are just examples of course. So much is possible! Outcross can be done safely and responsibly and is very useful when breeding animals. We know the advantages from the livestock breeding industry, a sector that generates a lot of knowledge on animal breeding. We can utilize that knowledge when breeding dogs. But knowledge is nothing if people won't work together. That is what is most important: to work together, with breeders, with vets, with scientists, with breed fanciers. After all, you can't manage an entire breed on your own, it takes all of us together.

With acknowledgement

David Cunningham, breeder of Irish wolfhound-like dogs in the United States.

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Gaby Bemelen, breeder of English mastiffs and mastiff crosses in the Netherlands.
https://www.hillsemastiffs.nl/

Jennifer Perry, breeder of English mastiffs and mastiff crosses in Australia.
https://www.facebook.com/GammonwoodMastiifs

LUA Dalmatian information: https://www.luadalmatians-world.com/enus/

Michael Hecht, owner of mastiff/greyhound/Irish wolfhound/malamute “Keeper”.
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