Domestication and coat colours

A review

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Contents

1   Abstract

The domestication of animals is a process of great interest to many scientific fields, including genetics. Differences in coat colour between wild and domesticated animals have been of scientific interest for a long time. Coat colours are easily recognizable phenotypes and so have been studied since the dawn of modern genetics. Many phenotypes that are similar across species have the same genetic basis, but there are numerous exceptions. Similar phenotypes within a species can also have different genetic backgrounds. The progressive advances in genetic research methodology have given new insights into both the molecular basis for coat colours and the history of domestication over the last decades. The variation in coat colours seen today is believed to be caused mainly by human selection.

Similarities in morphological changes between different species during domestication, including colour phenotypes such as white spotting, have long been noted. This is known as the domestication syndrome and two major hypotheses for this have been suggested: the neural crest hypothesis and the thyroid hormone hypothesis. This thesis gives an overview of the current knowledge about the genetic basis of coat colours in mammals, the genetic aspects of domestication of animals, and how the two are related.

Keywords: coat colour, domestication, genetics, pigmentation

2   Introduction

The research of domestication is a multi-faceted field that contains sciences as diverse as archaeology, anthropology, and biology. Different sciences can shed light upon the process from different angles and give a broader view of the shared history of humans, animals and plants. From a geneticist's point of view, the domestication process is a form of rapid evolution, and further understanding of domestication can also help advance our understanding of evolution.

Looking at mammals, it is easy to see that in wild animals, for most species all individuals have the same colouring, whereas many domesticated species show great colour variation (see examples in Figure 1). Variant colours that for example offer less camouflage or are less sexually attractive would be disadvantageous in the wild and therefore such mutations would not be able to spread (Reissman & Ludwig, 2013). There are also congenital problems linked to many coat colour variations, particularly in sensory organs, that would also be detrimental in the wild (Reissman & Ludwig, 2013). However, there also exist some wild mammals that show different colours. In the cat family *Felidae* 11 different species are known to have individuals

with an all-over dark coat, with jaguar (*Panthera onca*) possibly being the most famous example, where black individuals are often referred to as black panthers (Eizirik et al., 2003). Another example has been found in cave paintings in Peche Merle from the Paleolithic showing spotted horses. Genetic research has shown that genes for spotted phenotypes existed among horses in the Paleolithic, making it plausible that these are actual depictions of wild horses (Pruvost et al., 2011).
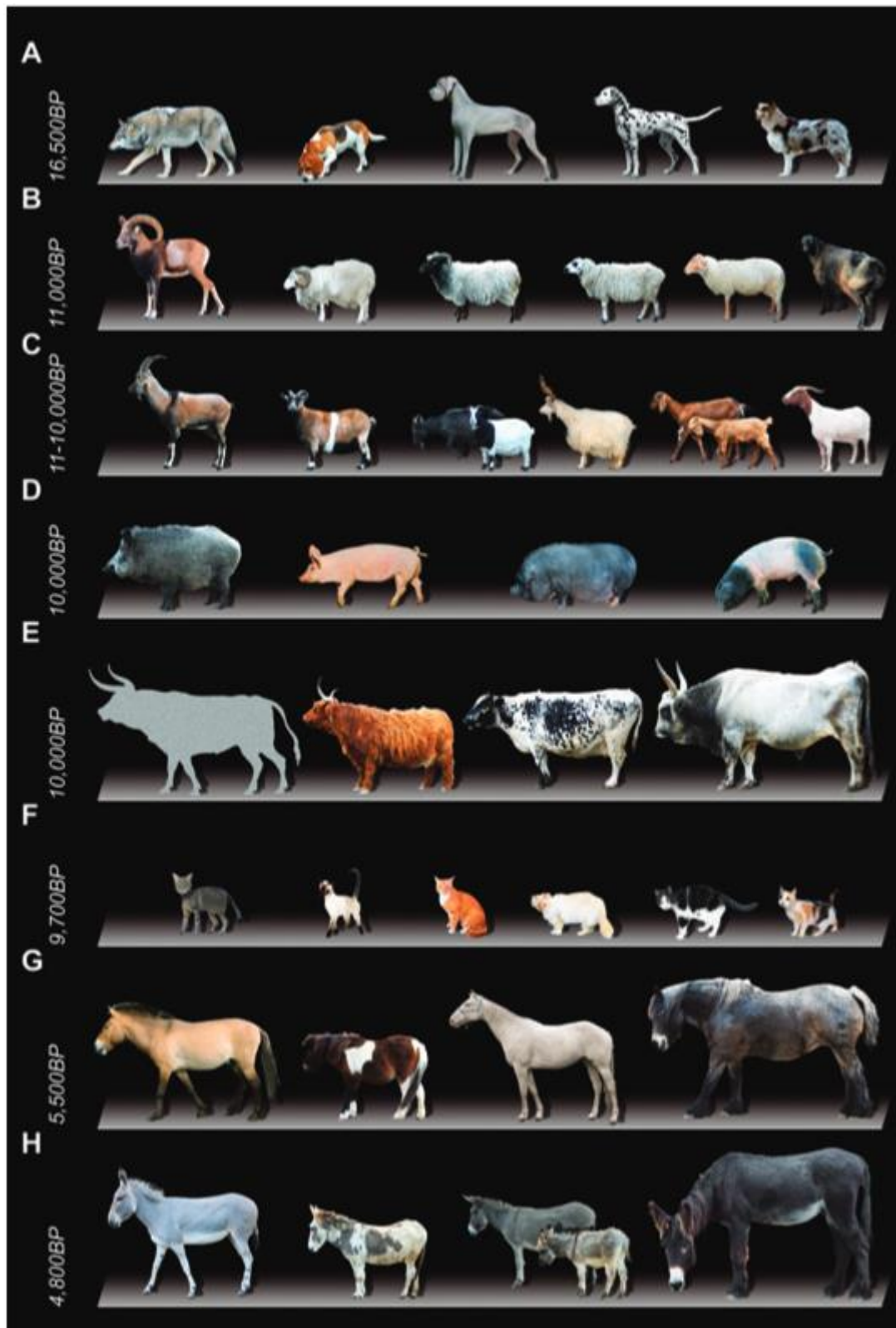
Figure 1. Examples of domesticated species. Wild ancestors in the left column and domesticated variants to the right. Approximate time of domestication at the far left. From Cieslak et al. (2011). Used with permission from the publisher.

At the beginning of animal husbandry, different coat colours could have been an advantage that made it easier to recognize the domestic individuals and discern them from the wild ones. For example, Fang et al. (2009) suggest that selection against camouflage patterns was important during the early days of pig husbandry, as pigs were often not kept enclosed but allowed to forage in the wild. A different coat colour offering less camouflage would have made it easier both to find the farm pigs in the wild and to distinguish the domestic pigs from wild ones.

Animals that have coat colours that differ from the most common have often been regarded as extra valuable or interesting by humans and sometimes connected to power. Many kings and emperors have been portrayed on white horses and white animals are not uncommon in heraldry (see Figure 2). A more current example is a white moose spotted in Sweden that made headlines all over the world (Gibbens, 2014).

It is also worth noting that the selection made by humans has not been made based on the same preferences over time (Cieslak et al., 2011; Wutke et al., 2016). This can be due to changes in cultural opinions on favourable traits as well as practical reasons when the use of domesticated species has changed. For example, the use of dogs has changed and diversified over time and in different cultures. It is reasonable that breeding for hunting dogs has involved selection for camouflage colourings, while more visible colours would have been more attractive in herding dogs.

During the last few centuries, animals have been bred even more selectively. The range of different breeds is vast in many species and often very specialized traits are selected for, as evidenced by stud books and breed standards that now regulate the preferences in phenotypes. For some breeds, only one colour phenotype is accepted and is sometimes even included in the name of the breed. For example, according to breed standards published by UK-based The Kennel Club (1994) a Golden retriever must have a gold or cream coat and no other colours are accepted. This gives some perspective on how selective humans often are when it comes to animal breeding.

Figure 2. White hart, badge of Richard II of England (National Gallery, 1395). Napoleon crossing the Alps (David, 1802). Charles I of England (van Dyck ,1633). Charles II of England (Lelly, 1685).

Humans sometimes attribute differences in behaviour to different coat colours in domesticated animals. Delgado et al. (2012) state that calico and tortoiseshell cats show more frequent aggressive behaviour towards humans than do cats of other colours, as reported by cat owners. This might mirror the owners' preconceptions and no definite support for coat colour influencing cat behaviour has be found so far. In other species, there are some cases of links between colour and behaviour, possibly due to congenital effects. Icelandic horses with silver coat colour have been considered being less mentally stable than individuals with other colours. In a test for fearfulness, silver-coloured horses were found to be more easily scared than Icelandic horses of other colours (Brunberg et al., 2013). This might be because a mutation in the silver gene (*SILV*) also causes a vision impairment in the horses (Bellone, 2010). In another study on horses, Finn et al. (2016) studied behaviour and reactions in chestnut and bay horses (see Figure 3), based on popular conceptions that chestnut horses are more difficult to train. No evidence was found that supported this notion.

Figure 3. Bay horse (left) from (Montanabw, 2006). Chestnut horse (right) from (Karlyne, 2006).

Similar studies on dogs have shown some correlation between coat colours and behaviour. In the English cocker spaniel breed, differences in dominant behaviour between dogs of different coat colours have been found (Pérez-Guisado et al., 2006) and a study on the Korean Jindo dog showed differences in fearfulness between individuals of different colour (Kim et al., 2010). Overall, correlation between coat colour and behaviour seems to be the exception rather than the rule, but this question has not been studied extensively and future research might change this standpoint.

With domesticated animals being an integral part of human life, further studies of the history of domestication may give insight not only in animal biology but also in human history. Since coat colour is a very easily observed phenotype, the genetics behind them has intrigued humans

for a long time. This review intends to give an overview of research in the genetics of coat colours in relation to domestication.

3   The molecular background of coat colour

Pigment cells in vertebrates have their origin in the neural crest (see Figure 4). This is a structure unique to vertebrates that is formed during embryogenesis. It is located along the axis that will later become the spine and consists of multipotent cells that create new cells of different types, including neurons and bones. Melanoblasts, which are a pre-stage of melanocytes, migrate from the neural crest to the epidermis and then into hair follicles. Once mature, the melanocytes synthesize melanins which are transferred into hairs (Huang & Saint-Jannet, 2004).
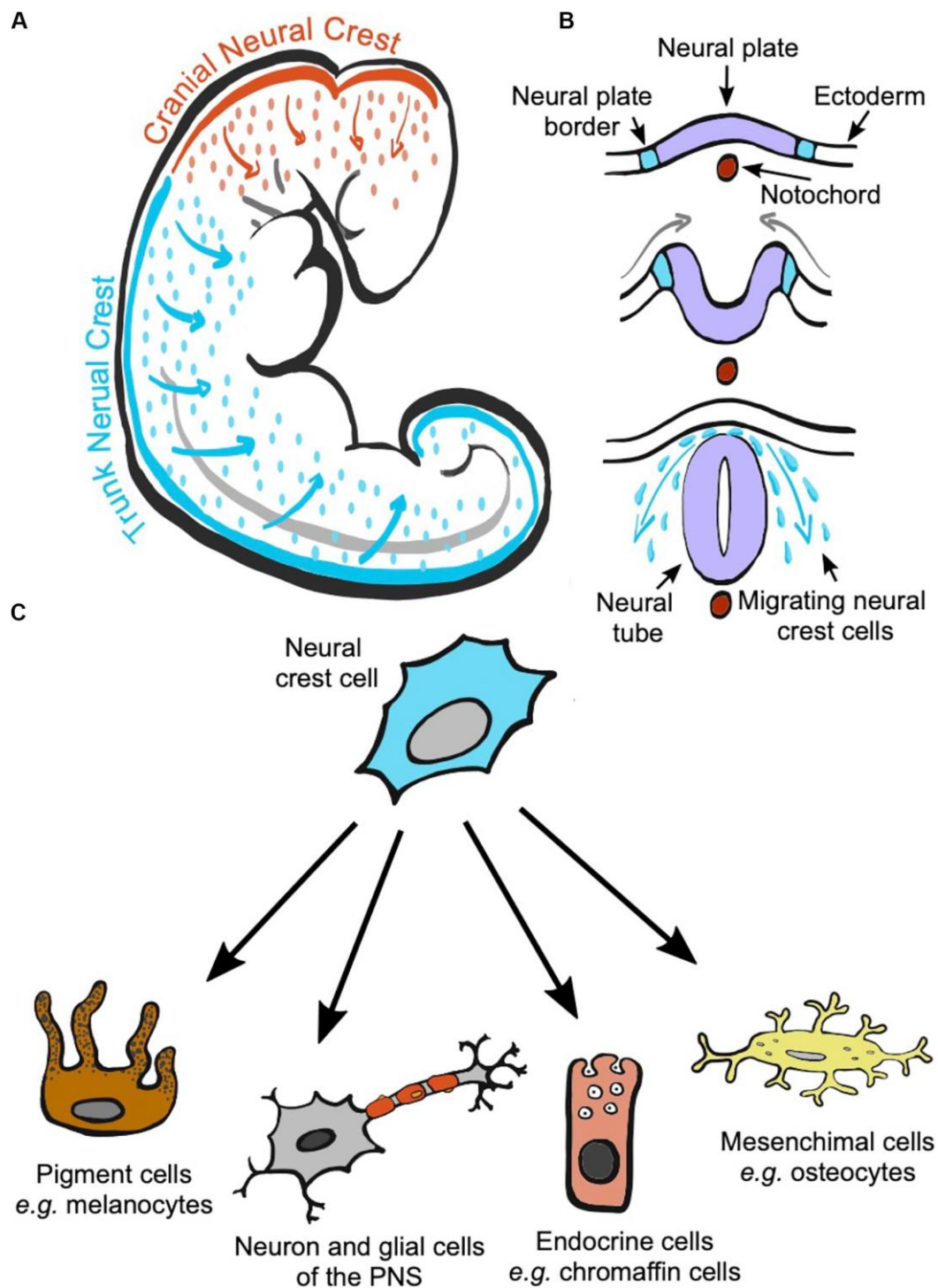
Figure 4. The neural crest and melanocytes. A: location of the neural crest in the embryo. B: development of the neural crest. C: neural crest cells migrate to different cell types. (San-Jose & Roulin, 2020. License: CC BY 4.0.)

3.1 Eumelanin and pheomelanin

There are two main categories of coat colour phenotypes: solid colour phenotypes and patterned phenotypes. Solid colours range from white to black and red. The red and black base colours are caused by the ratio between the two pigments eumelanin and pheomelanin. Patterned

phenotypes (e.g., striped and spotted) also show a specific colour based on the ratio of eumelanin to pheomelanin, but additional genes also result in patterning (Cieslak et al., 2011).

There are three loci that are responsible for the amounts of eumelanin and pheomelanin: *extension*, *ASIP* (or *agouti*) and *POMC* (Robbins et al., 1993; Barsh, 1996). The *ASIP* locus codes for agouti signalling protein (ASIP). The *extension* locus codes for the MC1R protein. *POMC* codes for Pro-opiomelanocortin, which breaks down into several smaller molecules, including melanocyte stimulating hormone (MSH). Even though MSH is important for pigment production, there seems to be no evidence of *POMC* mutations causing coat colour variations. ASIP, MC1R and MSH govern the production of melanins (see Figure 5). When MC1R binds to MSH, the level of eumelanin increases which produces a black/brown pigment. When MC1R binds to ASIP instead, the level of eumelanin is lower, so the relative amount of pheomelanin (red/yellow pigment) is larger (Robbins et al., 1993; Majerus & Mundy, 2003; Fontanesi et al., 2010). MC1R is known to cause black or dark phenotypes in many species including sheep (Våge et al., 1999), pigs (Kijas et al., 1998), dogs (Newton et al., 2000), mice (Silvers, 2012) and dromedaries (Alshanbari et al., 2019).
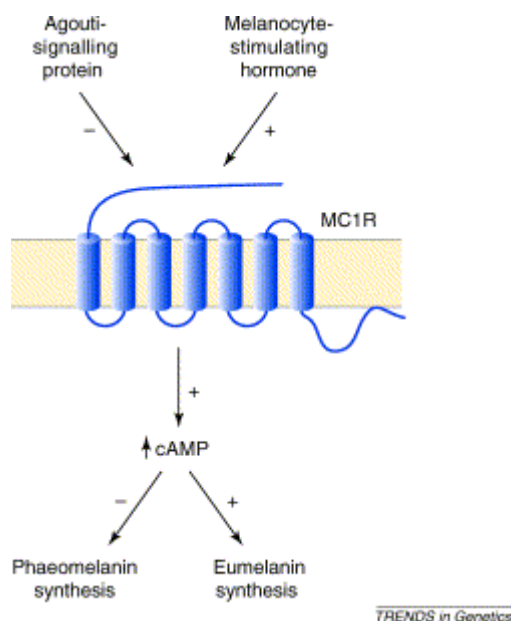

Figure 5. MC1R regulation. + denotes stimulation, - denotes inhibition. From Majerus & Mundy (2003). Used with permission from the publisher.

The *ASIP* locus also affects the hair pigmentation over time while the hair is growing. This occurs in cycles during the growth of the hair, giving each single strand of hair bands of lighter and darker colours (Figure 6). This is what gives many wild animals, e. g. wolves and wild rabbits, their typical grey and slightly mottled appearance (Figure 7) (Robbins et al., 1993).

Figure 6. Cat hair showing light and dark banding caused by the agouti-signalling protein. (Kersti, 2007).

Figure 7. Agouti-coloured domesticated rabbit. (Gerbil, 2007).

Loss-of-function mutations in *ASIP* can cause black phenotypes in cats (Eizirik et al., 2003), mice (Silvers, 2012), dromedaries (Alshanbari et al., 2019), dogs (Kerns et al., 2004) and horses (Rieder et al., 2001). A duplication in *ASIP* causes white coat in goats (Fontanesi et al., 2009) and sheep (Norris & Whan, 2008).

3.2   White and white spotting

3.2.1   The C locus

The most radical white phenotype in mammals is albino, showing as white coat and red eyes due to total lack of pigmentation. The albino colour has been known since the time of the Greek and Roman empires and was also the first trait in mammals to be confirmed to follow Mendel's laws of heredity (Seruggia et al., 2021). Albinism is caused by the recessive allele *c* at the *C* locus. The C locus codes for tyrosinase which is an enzyme that regulates melanogenesis, but the albino mutation in its homozygous state prevents tyrosinase production and so no melanin is produced (Jackson, 1994). There is no comprehensive list of all species with this trait, but

some examples in domesticated mammals are mice (Jackson, 1994), rabbits (Covrig et al., 2013), and cats (Schmidt-Küntzel et al., 2005). Albinism is also linked to visual and auditorial impairments (Barsh, 1996; Reissmann & Ludwig, 2013).

In horses, the *c* allele has never been found and there are no true albino horses. The recessive allele C^{cr} (cream) causes the production of tyrosinase to be lower, giving very little pigmentation but not a complete absence of melanin production. Horses homozygous for this allele have a white or pale-yellow coat with pink skin and blue eyes (Locke et al., 2001).

Another remarkable allele at the *C* locus is c^h (Himalayan) which makes tyrosinase heat sensitive. This prohibits melanin production in warmer body parts while pigmentation is intact in colder parts, e.g. feet and ears (Searle, 1990). The resulting phenotype is white with dark extremities, tail and face (see Figure 8) and can be seen in cats (Schmidt-Künzel et al., 2005), rabbits (Covrig et al., 2013), mice (Jackson, 1994), minks (Benkel et al., 2009) and in rare cases in dogs (Bychkova et al., 2021).

Figure 8. Himalayan rabbit. (Amber, 2013).

3.2.2   *KIT* and *EDNRB*

White-spotted phenotypes can be caused by mutations in the *KIT* gene (v-kit Hardy-Zuckerman 4 feline sarcoma viral oncogene homolog) that was first described by Yarden et al. (1987). KIT is a cytokine receptor, and its binding to the ligand mast/stem cell growth factor (MGF or SGF) is necessary for melanocyte survival (Jackson, 1994; Pielberg et al., 2002). Individuals with *KIT* mutations have normal melanin production, but the mutations can cause melanocytes to die before they have reached their destination in the hairs, and so white patches occur. This also explains why white patches are often found at the extremities in e.g. cats (David et al., 2014),

since these are the farthest away from the neural crest. In other species, other white patched phenotypes can be caused by *KIT* mutations, such as the white belt phenotype typical of some pig breeds (see Figure 9) (Giuffra et al., 1999).

Figure 9. Pigs of the British Saddleback breed, showing the white belt phenotype (AnemoneProjectors, 2012).

In horses, 22 different *KIT* mutations that cause different degrees of white spotting in horses have been found (Haase et al., 2007, 2009, 2011; Hauswirth et al., 2013; Haase et al., 2015; Dürig et al., 2017). This makes it impossible to determine a white-spotted horse's genotype from the phenotype alone (see some examples in Figure 10). Some of these mutations have only been found in a few individuals, and the molecular pathways leading to the different patterns have not yet been surveyed.
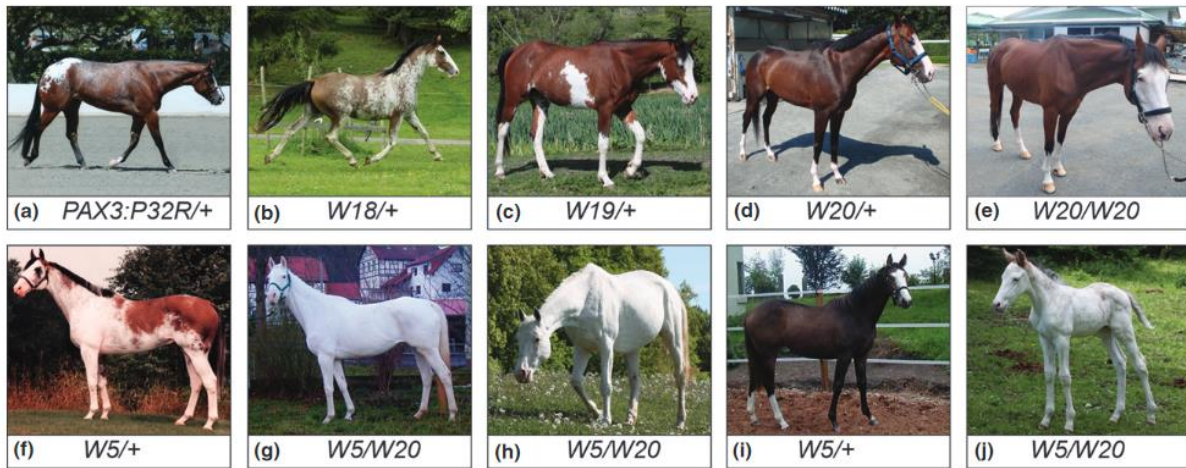
Figure 10. Different white patterns in horses, caused by KIT mutation. From Hauswirth et al. (2013). Used with permission from the publisher.

The *EDNRB* gene, coding for endothelin receptor type B (ET$_B$), can also cause white patches. A mutation of *EDNRB* consisting of a single amino acid change in the protein causes a significant white pattern named frame overo in heterozygotic horses (see Figure 11). Homozygotes for this allele die within a few days of birth from the so-called Lethal white foal syndrome, characterized by an all-white coat and non-functioning intestine due to absence of ganglionic cells (Yan et al., 1998). In mice, a strain called piebald-lethal have been shown to carry a mutation where the *EDNRB* gene is completely deleted, causing a similar phenotype of nearly completely white coat colour and life-threatening defects to the colon (Hosoda et al., 1994). Both melanocytes and ganglionic cells are derived from the neural crest (see Figure 4) and need ET$_B$ for their transfer, and these loss-of-function mutations stop the cells from migrating, resulting in an absence of pigmentation as well as lack of ganglionic cells in the intestine. Mutations in *EDNRB* have also been shown to cause white spotted phenotypes in pigs, although these are not linked with any congenital defects (Fontanesi et al., 2013).

Figure 11. Frame overo patterning. Note the position of white patches mainly on the sides, giving a frame of darker colour. From Pete Markham (2009).

3.2.3 Progressive greying

Most white or grey horses are born a darker colour and lighten over time. This is caused by a duplication in the *STX17* gene leading to upregulation of the gene, increasing production of Syntaxin 17 (Pielberg et al., 2008). The molecular background to this s not yet fully understood, but it is suggested that the gradual whitening of the coat is explained by the different life cycles of hair follicles and melanocytes. New hairs get their melanocytes from stem cells. When pigmentation of the new hair is finished, the melanocytes undergo apoptosis (programmed cell death). It is therefore possible to run out of melanocytes. The upregulation of *STX17* is believed to cause an increase in number of melanocytes, which might in turn cause premature depletion of the associated stem cells. The fact that grey horses often turn a bit darker before the whitening starts supports this (Pielberg et al., 2008).

Some dogs also show progressive greying. The genetic background of this is still unclear, but Schmutz & Berryere (2007) suggest that it is probably different from that of horses, based on the fact that greying horses show a higher frequency in skin tumours, which has not been found in greying dogs.

3.3 Sex-linked coat colours

Sexual heterochromatism is rare in mammals but an interesting exception is the sex-linked tortoiseshell colour in cats. Black coat colour in cats is caused by a dominant allele of *ASIP* producing eumelanin (Eizirik et al., 2003). The *orange* (*O*) locus responsible for production of pheomelanin is located on the X chromosome. The exact gene has not been found, but MC1R

has been ruled out since this is not found on the X chromosome (Grahn et al., 2005). The tortoiseshell phenotype (irregular spots of orange and black, see Figure 12) was an enigma early in the study of coat colour genetics. Bamber and Herdman (1932) concluded that orange is sex-linked which explains that only female cats show tortoiseshell colouring. With the colour gene on the X chromosome, each cell gets either the black or orange gene after X chromosome activation, as first described by Lyon (1962). There are rare occurrences of male tortoiseshell cats, but these have been shown to have a sex chromosome anomaly such as XXY (Leaman et al., 1999). X-linked tortoiseshell colour can also be observed in mice (Lyon, 1962). Similar phenotypes occur in a few other mammalian species, but for different reasons. In guinea pigs, tortoiseshell pattern is caused by a recessive gene and occurs in both males and females (Wright & Eaton, 1926) and the same holds true for rabbits (Punnett, 1924).
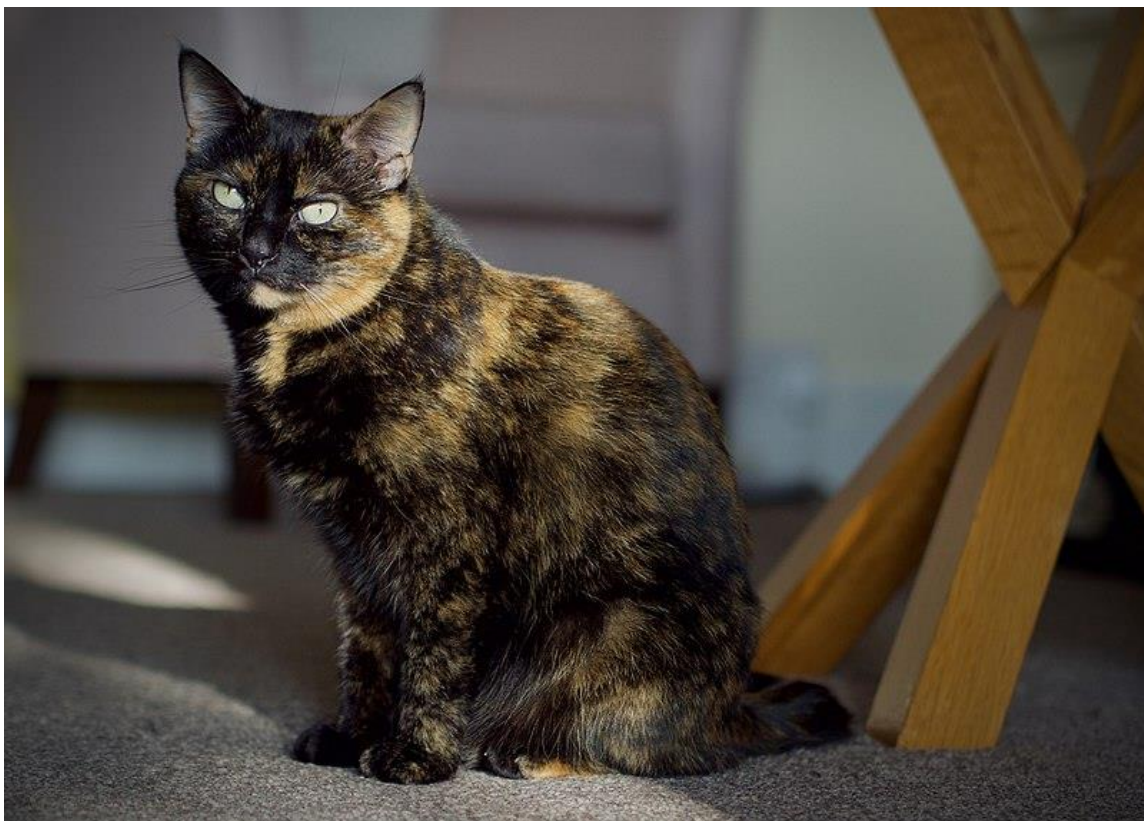

Figure 12. Tortoiseshell cat. (DrTimG, 2019).

4   The process of domestication

Not all species were domesticated in the same way and for the same reasons. The way to domestication can be separated in to three pathways: commensal, prey and directed (see Figure 13). The commensal pathway starts with animals being attracted to humans, possibly for the chance to feed off human waste. As humans saw benefits of the relationship with the animals, the process became more intentional. The prey pathway starts with animals being hunted by

humans and the humans subsequently capturing and breeding the animals for food. The directed pathway is even more intentional and refers to animals being captured specifically for breeding, often to be kept as work animals or pets (Zeder, 2012; Larson & Burger, 2013).
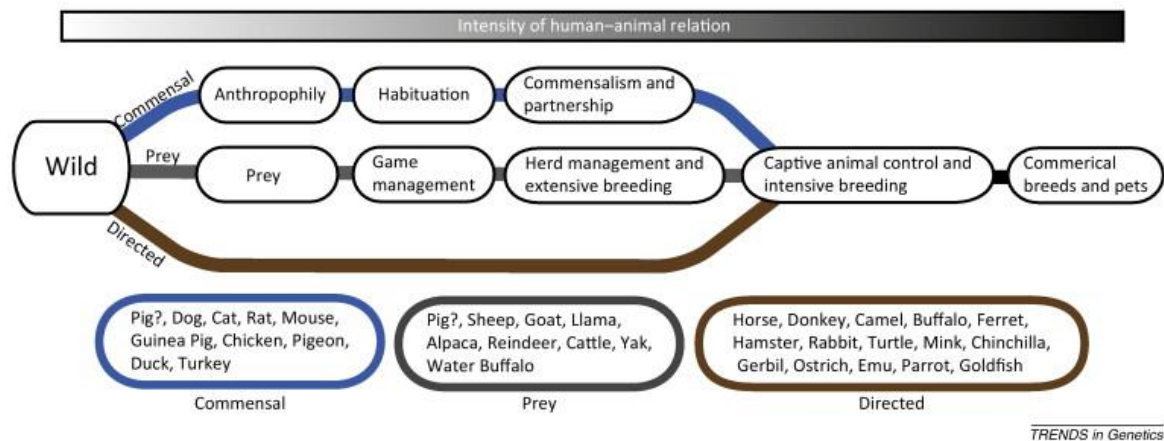

Figure 13. Pathways of domestication. From Larson & Burger (2013). Used with permission from the publisher.

The first species domesticated by humans was the dog, which was a companion to humans at least 15000 years ago. This is an example of the commensal pathway. The large increase in domestication of animals happened during the Neolithic period (about 10000-4500 BC) and is associated with the human transition from hunting and gathering to farming in the Old world. Domestication of different species took place in different times and places (see Figure 1), and it is still unsure in many cases whether the domestication of a single species happened only once or on several occasions (reviewed by Cieslak et al., 2011). For example, seven different potential locations for domestication of the pig have been identified (Larson et al., 2005). Dobney & Larson (2006) state the difficulties in determining the original place for domestication by imagining the ideal dataset: it should include DNA from modern domesticated and wild populations, but also archaeological samples from both wild and domesticated individuals from different times and places. Even with such an extensive dataset, the authors argue, it would not necessarily be possible to draw unequivocal conclusions.

It is not unproblematic to think of wild and domesticated as a dichotomy between wild and domesticated. There is a spectrum between the two and overlooking this might obstruct the understanding of the domestication process (Dobney & Larson, 2006). For example, in some regions it is not uncommon for domestic pigs to roam freely during the daytime. Due to this, these pigs could be considered a bit less domesticated than animals that are always kept captive by humans. Furthermore, it gives the possibility of hybridization with wild boars (Rowley-Conwy et al., 2006).

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Since domestication started with removing a small group of animals and breeding from them, inbreeding is common and genetic diversity is reduced. It is suggested that all domesticated species were affected by genetic bottlenecks at one point or another, but that variation in coat colour can appear after only a few generations. Artificial selection for these traits is thought to have started shortly after the domestication process began and is responsible for the great variation in phenotypes seen today (Cieslak et al., 2011).

4.1 The domestication syndrome

A famous and influential study on foxes was initiated in the 1950s by Russian researcher Dmitri Belyaev and is still ongoing today. Breeding foxes for tameness, as a sort of rapid domestication process, resulted in variations in their physical appearance, not only in coat colour but also in body shape, after just a few generations (Belyaev, 1979; Trut et al., 2009; Dugatkin, 2018). This was in line with observation by Darwin et al. (1868) of traits that were shared by many domesticated species, e.g., variation in colour, short snouts and floppy ears. This has later been dubbed the domestication syndrome.

It has been suggested that thyroid hormone is the cause of the domestication syndrome, based on similarities between symptoms of hypothyroidism (lack of thyroid hormone) and traits in domesticated animals (Crockford, 2004). Since thyroid hormone plays a role in melanin production (Crockford, 2004), this could be relevant to the coat colour aspect of the domestication syndrome. There is some agreement that the endocrine system is probably of importance with regards to domestication. However, due to the complexity of the endocrine system and the fact that thyroid hormone is vital in most aspects of development, it is unlikely that there is any one gene related to hypothyroidism that is also responsible for the domestication syndrome, but rather that causes might be found in factors regulating gene expression (Rowley-Conwy et al., 2006).

Wilkins et al. (2014) proposed that most of the morphological effects of domestication can be explained by differences in neural crest cell development. The authors argue that this can cause reduction in adrenal and sympathetic ganglia, in turn causing reduced stress and fear which could be what is selected for when breeding for tameness. At the same time, the same neural crest cell gene variations can cause morphological variations in coat colouring, skull shape, ear size and other aspects connected with domestication syndrome (Wilkins et al., 2014). This could explain the results of the experiment started by Belyaev (1979) and be of interest for future studies in connections between coat colour and other traits. A study on guinea pigs showed lower stress levels, less aggressiveness and more social behaviour in domesticated individuals

compared to wild ones, which supports this hypothesis (Künzl & Sachser, 1999). Similar findings have been made in cats (Montague et al., 2014), horses (Librado et al., 2017), dogs (Pendleton et al., 2018), and foxes (Wang et al., 2018).

The idea of domestication syndrome and the findings of the Russian farm-fox experiment (Belyaev, 1979; Trut et al., 2009; Dugatkin, 2018) have also been challenged. Lord et al. (2020) argue that the conclusions drawn from this experiment are highly overstated. Going through literature in the field, the authors find that there is no entirely common definition for what constitutes the domestication, but that different sources list different traits and that no one trait is listed in all the sources examined. Lord et al. (2020) also argue that the sample size is too small and that the fact that the original foxes were not wild but had been bred for fur over several decades undermines the findings of the project. However, differences in coat colour are the most commonly reported morphological change in the sources scrutinized by Lord et al. (2020) and so it is plausible that even if the domestication syndrome is not as universal as previously proposed, changes in coat colour can still be considered markers for domestication.

To further investigate the domestication syndrome, Hansen Wheat et al. (2020) conducted a study on dog breeds. Data from standardized behavioural assessments of more than 76000 dogs were used. The 78 different breeds represented in the dataset were assessed for three morphological traits associated with domestication syndrome: white pigmentation, floppy ears, and curly tails. The correlation between these traits and the behavioural assessment, and also between the three morphological traits, was then examined. The authors found no significant correlations, i. e. the morphological traits do not predict behaviour and there is no covariation between white pigmentation, floppy ears and curly tails. This puts the idea of a common cause for the domestication syndrome in question. However, as the authors note, it is possible that alleles that covaried at the point of domestication have later decoupled (Hansen Wheat et al., 2020).

5   Ancient genomics

One of the biggest game changers in the field of genetics and domestication has been the rise of ancient genomics. Thanks to improved DNA excavation and sequencing methods, many whole ancient genomes have been sequenced. So far, more than 450 specimens of old findings of domesticated species have been genome sequenced and published (Frantz et al., 2020).

Previously, genetic isolation of domestic populations has been emphasized as a cause for genetic differences between wild and domestic animals. Often it has been assumed that the first

domestication events included very few individuals, leading to a founder effect that would have resulted in low genetic diversity in the domesticated population. The genetic diversity now seen in domesticated species would all have arisen from mutations and selection within the population. However, genomic records from old species now imply that introgression from wild populations may have happened on several occasions for many species (Frantz et al., 2020). The fact that the domesticated population still show genetic and phenotypical differences to their wild counterparts can be explained by so called *islands of domestication*, a smaller set of loci that has a large effect on the phenotype (Turner et al., 2005).

The notion that all domesticated populations have had genetic bottlenecks is also challenged. Two studies on dogs show that the major part of loss of genetic diversity happened over the last few centuries and not early in domestication (Frantz et al. 2016; Botigué et al. 2017).

Ancient genomics have also highlighted that human preferences, and thus human selection, sometimes change over time. In a study by Wutke et al. (2016), ancient bones from a total of 201 horses were sampled and their colour phenotypes studied. This showed that spotted phenotypes (e.g. leopard spotted, see Figure 14) had become increasingly more common in Copper age and Iron age, but that in the Medieval period, these alleles had become rarer and solid colour chestnut horses were the most common. This is attributed mainly to cultural changes in human preference. For example, advances in weaponry such as the development of the longbow might have given a disadvantage to spotted horses in warfare, since they would have been easier to spot from a distance (Wutke et al., 2016). Selection against spotted horses may also have been a side effect of deliberate selection against visual impairments, since homozygosity for leopard spotting is linked with congenital stationary night blindness in horses (Bellone, 2010).

Figure 14. Leopard spotted horse. From Karakal (2007).

6 Conclusions

There are many links between coat colour and domestication in animals, although the causes and effects are not entirely understood. The molecular background of coat colours is generally well understood and there are many similarities across species. The reason that we see such a large variety of coat colours in domestic animals compared to their wild ancestors is mostly human selection. This is partly because of humans' interest in the extraordinary, but it is also probable that coat colour variation has been caused by selection for other traits such as docility. Great advancements in ancient genomics have given further insight in this.

There is still work to be done, however. The study of domestication is a broad subject, and many branches of science can help improve the understanding. Genetics can play an important role and new advances in sequencing of ancient genomes can provide more information about the molecular history of animals. Furthermore, development of new bioinformatic tools can help get even more information out of already sequenced material. There also seems to be little research done on epigenetics in relation to domestication, and more work in this area could be important especially in the understanding of the domestication syndrome. Although reasonable hypotheses about its origin have been provided, it is reasonable to think further investigation of gene expression and regulation could lead to a broader understanding of the domestication syndrome and perhaps provide convincing support for one hypothesis over another.

7 Societal and ethical considerations

Knowledge about the domestication process can be valuable in improving the care of livestock. Understanding how animal behaviour has been affected by domestication can help in creating better living conditions for today's domestic animals, for example to give animals possibilities to engage in their natural behaviour. In the future, domestication of further species might be necessary to produce enough nourishment for a growing world population. Knowing what has happened in previous historic domestication events could hopefully be beneficial to both humans and new domesticates.

Understanding the joint history of humans and animals can also give insight into the relationship between man and nature on a grander scale. This can be relevant to discussions about human impact on ecosystems, and help us handle future challenges, not least caused by climate change.

This being a literature review, no harm has been inflicted to any animals. However, human's interest in new coat colours can have considerable economic ramifications in animal breeding. Genetic understanding of coat colour variation could be a double-edged sword here. Knowledge

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about detrimental congenital effects associated with certain coat colours could lead to breeders taking care to avoid these effects which would lead to better lives for domestic animals. However, new discoveries in the origin of new coat colour variation could also lead to unscrupulous breeding that favours economic value over animal welfare.

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