How could colouration affect behaviour in animals?

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Abstract

Domestication, the process when animals adapt to captivity, tends to modify the phenotype towards what is known as the “domesticated phenotype” which includes changes in reproduction, behaviour and morphology. One of the first and more striking changes is a loss of pigmentation in the coat colour, causing a white patterned plumage, skin or fur. There are many studies reporting on associations between behaviour and coat colour in different species. In general dark pigmented animals are described to be more aggressive, dominant and sexually active. There are two different types of melanin pigments, red-yellow pheomelanin and black-brown eumelanin. The melanocortin-system regulates colouration by switching the production between pheo- and eumelanin. Melanocortins also bind to receptors responsible for several physiological and behaviour functions, and therefore offers a good model to explain the relationship between colouration and behaviour. Another explanation could be the close relationship between eumelanin and dopamine, a neurotransmitter known for its general effects on physiological and behaviour responses. It is also important not to forget the significance of underlying genetic effects such as linkage or pleiotropy, which could be the third explanation for the relation between two such complex traits. However, what ever causes the effects the association between behaviour and pigmentation seems to be a widespread phenomena in the animal kingdom and it is as fascinating in insects as in birds and mammals.

Definition of domestication

Domestication, the process by which captive animals adapt to man and the environment he provides (Price, 1999), is defined in a various numbers of ways. Rindos (1980) postulate the domestication as a symbiotic evolutionary process between humans and animals or plants, where the domestication occurs before the origin and development of agricultural systems and is the reason agricultural system develops. Contrary, Hale (1969)
and Clutton-Brock (1977) simply suggested domestication to be a condition in which breeding and feeding of animals are more or less controlled by man. Already in the 19th century Darwin (1859; 1868) suggested domestication to be more than taming, that it includes breeding animals in captivity, is goal-oriented, may occur without conscious effort on the part of man, increases fecundity, may bring about atrophy of certain body organs, enables animals to achieve greater plasticity, and is facilitated by subjugation to man, the domesticator. So far, definitions of domestication regarded the environmental circumstances that the animal experiences. However, in 1984 Price also added the genetic factor to the definition when he described domestication as “that process by which a population of animals becomes adapted to man and the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation”.

The domesticated phenotype
Domestication is a developmental phenomenon that offers a good model for studying evolution. Price (1998) described three central processes in domestication; relaxation of natural selection, intensified selection of traits preferred by humans and natural selection under captivity leading to adaptation. The adaptation of captive animals to their environment tends to modify the morphology and other traits of animals towards what has been termed “the domesticated phenotype” (Price, 1998; Jensen, 2006). In summary, the domestic phenotype differ from its wild ancestor by having a different colour of fur, skin or plumage, being brachycephalic and chondrodystrophic, having a reduced brain size, develop faster with increased reproductive capabilities, being less fearful and more sociable (Jensen, 2006). The change in coat colour is among the first responses due to adaptation, and probably also the most striking one. During domestication the proportion of white or spotted animals in the population increases rapidly (Price, 1998). Studies have shown that colour phenotype may be linked to behaviour selected during domestication. The most famous example comes from “the farm-fox experiment” where Dmitry K. Belyaev in the late 1950s started to select silver foxes (Vulpes vuples) for one single behavioural trait, tameness, and created a population of tame foxes. The first notable change that occurred was loss of pigmentation in certain areas of the body creating the so
called piebald coat colour. This colour pattern is today shared among numerous domestic breeds such as dog, pig, horse and cow (Trut, 1999).

**Pigmentation in relation to stress**

The loss of pigmentation, hypopigmentation, occurring as a side effect during domestication could indicate that low pigmented phenotypes adapt easier to cope with the stress of captivity. There are studies of mink and sables that further support this theory, where randomly bred non-pigmented individuals have been described as “naturally tame” in comparison to dark pigmented individuals when handled by humans, even without any selection for tameness (Keeler and Moore, 1961; Trapezov et al., 2008). In a literature review of pleitropic effects on behaviour and colouration in wild populations of vertebrates, Ducrest et al. (2008) conclude that darker wild vertebrates are more aggressive and sexually active than lighter individuals, but in contradiction, also more resistant to stress than lighter individuals. This is in line with results from studies of Atlantic salmon and rainbow trout where selection for divergent hypothalamus-pituitary-interrenal responsiveness caused a change in dermal pigmented patterns. The skin of salmon and trout varies from non-pigmented to densely spotted by black-brown eumelanin (see below) formed in eumelanin-producing chromatophores. Individuals selected for low-responsive (LR) post-stress cortisol levels exhibited more spots per cm² than individuals from the high-response (HR) line. Further, LR individuals showed a reduced physiological and behavioural response to stress, compared to individuals from the high-responsive strain, when subjected to a series of behavioural tests measuring stress response (Kittilsen et al., 2009).

Recently, measurements of cortisol levels were done in hair from dogs and interestingly, differences in cortisol levels in different coloured hairs from individual dogs were observed. Red-yellow (pheomelanin) hairs were

![Fig. 1 Example of pigmentation in a Red junglefowl male with red pheomelanin feathers and black eumelanin feathers.](image)
consistently higher in cortisol levels than black-brown (eumelanin) hairs, with banded, striped bars (agouti) hairs as intermediate (Bennett and Hayssen, 2010). Dogs are animals with a wide range of different coat colours and patterns. In some breeds associations between coat colour and behaviour have been reported. One example comes from the English Cocker Spaniel where significant differences in dominance have been shown to depend on coat colour. Dogs with golden, black and particolour coats differ in dominance where individuals with a golden coat colour are more dominant than particoloured ones, with black as intermediate (Pérez-Guisado et al., 2006). Another example comes from the Jindo dog, a Korean native breed. The dogs were exposed to a battery of behavioural tests measuring social, aggressive, fearful and submissive reactivity and the results suggested that Jindo dogs with fawn coat colour show a lower intensity of fearful behaviours and submissive reactivity than those of white coat colour (Kim et al., 2010). Taken together, these studies from dog reflect the complexity of pigmentation in relation to behaviour where the question is not only if the animal is pigmented or not, but also the degree of pigmentation and moreover the type of the pigments causing the coat colour (e.g. eumelanin or pheomelanin, see below).

To conclude so far, the majority of studies presented above show that pigmented individuals could be associated with lower cortisol response. This is in contradiction to the hypothesis that hypopigmentation would be an effect of domestication that has appeared because hypopigmentation is linked to lower stress response and hence, low pigmented phenotypes would adapt easier to captivity. Therefore, one could speculate that loss of pigmentation is trait directly selected by man as suggested by Fang et al. (2009).

The melanocortin theory
There are two different types of skin and hair pigments; brown-black eumelanin and yellow-red pheomelanin (Fig. 1). Melanin based colouration is mainly controlled by the transmembrane G-protein-coupled melanocortin 1 receptor (MC1R) and its melanocortin agonist, melanin-stimulationg-hormone (α-MSH) and antagonist, the agouti protein. Circulating α-MSH activates MC1R, located in the melanocytes, which causes an
intracellular increase in cyclic AMP. A signaling cascade affecting the activity of eumelanin-enzymes is induced, resulting in a deposition of black-brown eumelanin pigments in the melanosomes (Fig. 2). The binding of agouti signaling protein (ASIP) to MC1R causes a decrease in cyclic AMP levels that switches the production from eumelanin to yellow-red pheomelanin (Fig. 2). There are five different types of melanocortin receptors (MC1-5R), well conserved among vertebrates, with various locations (e.g. pituitary, adrenal and exocrine glands, reproductive tract, CNS, muscle, immune cells, adipose tissue) responsible for diverse physiological and behavioural functions. Moreover, there are three types of melanocortins (α-, β-, γ-MSHs) which all binds to the five types of MCRs. The melanocortin system is suggested to have pleiotropic effects on pigmentation and behaviour due to the widespread location and action of the melanocortin receptors and their ligands (Ducrest et al., 2008). This system is also suggested to cause the differences in behaviour and hormone levels in the studies of salmon/trout and dogs/dog hair, mentioned above (Ducrest et al., 2008; Kittilsen et al., 2009; Bennett and Hayssen, 2010; Kim et al., 2010).

![Diagram of melanogenesis](image)

**Fig. 2** Outline of melanogenesis. (A) α-MSH binds to the MC1R receptor causing an increase in cAMP that triggers a signaling cascade resulting in a deposition of eumelanin in the melanosomes. (B) The agouti signaling protein (ASIP) acts as an antagonist and blocks the cAMP signaling within the melanocytes. The decrease in cAMP alters the synthesis and switches the production from eumelanin to lighter pheomelanin. Redrawn from (Tully 2007).
In addition, there are several studies in mice and rat that have shown a relation between the agouti gene and behaviour, where nonagouti individuals are described as less aggressive, less active and easier to handle than their agouti counterparts (Keeler, 1942; Keeler and Dean King, 1942; Cottle and Price, 1987; Hayssen, 1997).

The PMEL17 gene and Dominant white allele

However, there is another pigmentation regulating gene that has been suggested to exert pleiotropic effects on behaviour in chickens, the *PMEL17* gene. *PMEL17* is not directly involved in the melanin synthesis (Theos et al., 2005), but is located in the vesicular structures of premelanosomes and plays an important role in the maturation of premelanosomes into melanosomes (Raposo et al., 2001). The *PMEL17* protein is essential in the amyloid fibril formation that occurs during premelanosome maturation (Huff et al., 2003), and serve as the site of melanin deposition (Yasumoto et al., 2004). Chickens with a white plumage have a 9 base-pair insertion in exon 10 of the *PMEL17* gene, known as the Dominant white allele, which causes a dysfunctional transmembrane region in the protein and unable melanin deposition. Therefore, chickens homozygous for the Dominant white allele have no mature eumelanosomes, and show a completely non-pigmented plumage (Fig. 3). A QTL-study of an intercross between Red junglefowl (considered to be the ancestor of all domestic breeds) and White Leghorn (selected for egg laying) identified a QTL for the behaviour feather pecking that coincided with the *PMEL17* gene (Keeling et al., 2004).

The dopaminergic theory

Feather pecking is a behaviour among different species of fowl, where feathers are

![Image](https://via.placeholder.com/150)

*Fig. 3* White leghorn males lack pigmentation in the feathers due to the Dominant white mutation in the *PMEL17* gene. The mutation also seems to protect against feather pecking.
pecked at or removed from one bird by another. This abnormal behaviour may further lead to cannibalism and is therefore a severe well fare problem often seen in the poultry industry (Dixona, 2008). Studies of individuals selected for being homozygous for either the wild type allele or Dominant white showed that pigmented wild type individuals were more exposed to feather pecking than non-pigmented Dominant white chickens (Keeling et al., 2004). This was confirmed by Nätt et al. (2007) who not only showed that homozygous wild type females were more exposed to feather pecking than homozygous Dominant white females, but also that the genotypes seemed to differ in mainly social behaviour. Nätt et al. (2007) suggested one possible theory on how the PMEL17 gene could exert its effect on behaviour; melanin is synthesised from tyrosine and uses dihydroxyphenylalanin (DOPA) as a close precursor. DOPA is also used in the production of catecholamines (dopamine, epinephrine and norepinephrine) which are all well known to affect behaviour and physiological responses (Fig. 4). An accumulation of eumelanin due to the PMEL17 mutation could alter the biochemical equilibriums and thereby the concentrations of different catecholamines, that in turn would affect behaviour (Nätt et al., 2007).

![Figure 4](image.jpg)

**Fig. 4** The melanin synthesis (to the left) is closely related to the catecholamine synthesis (to the right) through dihydroxyphenylalanin (DOPA) from which both eumelans and catecholamines (dopamine, nor epinephrine and epinephrine) are synthesised.
The dopaminergic theory in Drosophila

Not only mammals and birds are in focus for studies of behaviour in relation to pigmentation. Associations between colouration and behaviour have been seen in insects as well. In Drosophila melanogaster individuals that lack function in the yellow \((y)\) gene show a hypopigmented phenotype. The gene has also been shown to affect courtship behaviour in males (Drapeau et al., 2003). The authors suggest a similar theory to the one presented by Nätt et al. (2007) on how the gene affects behaviour. The \(y\) gene acts genetically downstream from the \(fru\) gene, which is known to alter the levels of one component of the male courtship ritual, the wing extension. \(Fru\) and \(y\) mutants show reduced levels of wing extension during courtship and both genes have been detected in the region in brain that is necessary for development of that behaviour. The \(y\) gene is also known to affect melanisation and \(y\) mutants show a decreased melanisation over much of their body cuticle, making the flies yellow/golden brown (Drapeau et al., 2003). Drapeau et al. (2003) speculate that “\(y\) mutant behavioural defects are related to abnormal levels of dopamine (DOPA), because DOPA and melanin are synthesized from tyrosine in the same basic biochemical pathway and are similar molecules”.

There is a number of other studies in Drosophila that strengthens the theory of a relationship between pigmentation and behaviour through dopamine. A study that adds to this was performed by Hodgetts and O'Keefe (2006) who studied the Dopa decarboxylase gene (\(Ddc\)). The enzyme (\(DDC\)) catalyzes the conversion of Dopa to dopamine and 5-hydroxytryptophan to serotonin and is expressed in both neural and epidermal cells. Dopamine and serotonin receptors are located in the CNS in embryonic, larval and adult stages of Drosophila. Mutations in \(Ddc\) eliminate both dopamine and serotonin within their respective neurons and, not that surprisingly, the \(Ddc\) gene has been shown to be crucial for both behaviour and development in Drosophila. DDC further plays a central role in epidermal cells for cuticle maturation and is necessary for a proper abdominal pigmentation (Hodgetts and O'Keefe, 2006).

Geneticists have also studied the genes tan and ebony which are both connected to pigmentation alterations and abnormal levels of dopamine. Individuals of Drosophila
with a mutation in \textit{tan} show a light phenotype and abnormal low dopamine levels whereas \textit{ebony} mutants are highly pigmented with an excess of dopamine (Drapeau et al., 2003; Hodgetts and O'Keefe, 2006). Taken together, the studies from \textit{Drosophila} provide some evidence for a relationship between pigmentation and behaviour through the dopaminergic system. If this theory is applicable for other species remains to be investigated, however it is tempting to believe that this could explain some of the pigmentation related differences seen in the \textit{PMEL17} chicken (Keeling et al., 2004; Nätt et al., 2007).

\textit{Behaviour associated to pigmentation in other invertebrates}

In addition to the studies of \textit{Drosophila} there are other examples from the invertebrates showing similar associations between pigmentation and behaviour as in mammals. Female paper wasps show a big variation in size and shape of black spots on the face. The spots have shown to be strongly correlated with overall body size. Further, the facial patterns also predict social dominance, with more dominant wasps having more spots (Tibbetts and Dale, 2004).

The desert locust has been studied in relation to ecological processes. An increase in the population density can result in a transformation of solitary living individuals into gregarious, swarm-forming locusts. With this transition comes a striking colour change where green solitarious-phase juveniles becomes black gregarious-phase juveniles with a black and contrasting yellow or orange background colour (Sword et al., 2000).

Insects and reptiles are ectothermic organisms that rely on external heat sources to control body temperature. In a study by Forsman et al. (2002) Pygmy grasshoppers of two different colour morphs (pale versus dark) were exposed to experimental situations imposing a trade-off between temperature regulation and feeding. The results showed a significant difference in behavioural thermoregulation between dark and pale females, where pale individuals spent more time feeding than dark ones, regardless if feeding was associated with a risk of either hypothermia or overheating (Forsman et al., 2002).
**Pleiotropic effects and linked genes**

Kronforst et al. (2006) report that *Heliconius* butterfly males with yellow coloured wings prefer to mate yellow coloured females. It is suggested that this behaviour could be a pleiotropic effect or an effect of linked genes (Kronforst et al., 2006).

Pleiotropy is the phenomenon where one single gene controls for multiple phenotypical traits. One well known example of pleiotropy comes with the *frizzle* gene in chickens. The *frizzle* gene not only causes feathers that are curled outward the body of the bird, but also affects body temperature, metabolic and blood flow rate and increases digestive capacity (Lobo, 2008a).

Linked genes are two genes closely located to each other on the chromosome, and therefore often inherited together. The phenomenon of genetic linkage was discovered through studies of heredity in fruit flies by Thomas Hunt Morgan, who noticed that the eye colour in the fly was associated with sex and therefore must be linked (Lobo, 2008b).

Pleiotropy and linked genes, as an explanation for associations between pigmentation and behaviour, are other important factors to consider. Another example where the pleiotropic effects or linkage is suggested to be the causative factor, once again, comes from the *Drosophila*. In *D. elegans* the males posses a wing melanin spot and stereotypical wing display element in courtship behaviour, whereas *D. gunungcola* lacks both. These two complex traits have in some way evolved and become coordinated during evolution. Using F1 male hybrids it was shown that the locus or loci for wing spot formation is located at the X-chromosome and the loci for courtship display on the autosomes. In a backcross progeny it was further shown that male wing spot size and courtship wing display are highly correlated, suggesting that linkage or pleiotropy may have been involved in their coordinated evolution (Yeh et al., 2006). It is important to take into consideration the genetic architecture underlying such complex traits as behaviour and pigmentation. It is difficult to discover weather pigmentation and behaviour is due to underlying genetic mechanisms such as pleiotropy and linkage, since the two traits are so
complex and therefore difficult to tear apart. This emphasizes the importance of genetic studies in addition to physiological and behavioural measurements.

**Conclusions**

Pigmentation and behaviour are two very complex traits to study. Results from a wide range of species have shown that behaviour can be associated to pigmentation, that it is not only as a question of whether the individual is pigmented or not, but moreover the degree of pigmentation and also type of pigmentation. There is not yet convincing evidence to explain the relation between colouration and behaviour, but from the literature three main theories can be drawn; 1) the wide distribution and function of melanocortins, not only regulating colouration but also responsible for several physiological and behavioural functions, 2) the close relationship between melanin and dopamine, that are both synthesized from tyrosine in the same basic biochemical pathway, 3) the underlying genetic architecture such as pleiotropy or linked genes that have caused a coordinated evolution. It is difficult to study either of the two complex traits, and therefore it is a challenge to discover the responsible mechanism. However, the association between behaviour and pigmentation is a very intriguing phenomenon well worth to investigate, not only for better understanding on how different traits can be related, but also for the applicability in an animal well fare perspective such as feather pecking.
References


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