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Review

# Coloration in Mammals

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**Mammalian colors and color patterns are some of the most diverse and conspicuous traits found in nature and have been widely studied from genetic/developmental and evolutionary perspectives. In this review we first discuss the proximate causes underlying variation in pigment type (i.e., color) and pigment distribution (i.e., color pattern) and highlight both processes as having a distinct developmental basis. Then, using multiple examples, we discuss ultimate factors that have driven the evolution of coloration differences in mammals, which include background matching, intra- and interspecific signaling, and physiological influences. Throughout, we outline bridges between developmental and functional investigatory approaches that help broaden knowledge of mammals' memorable external appearances, and we point out areas for future interdisciplinary research.**

## Highlights

Mammalian external appearances are well known and their developmental and adaptive significance are under active study.

Pigment regulation and pigment patterning determine how hair color develops.

Mammalian hair and skin color can change during an individual's lifetime.

Most mammals have dichromatic vision but some monkeys and apes are trichromatic which may influence pelage coloration involved in signaling.

Most mammals, both prey and predators, are assumed to match their background. Nonetheless, diverse and anachronistic color patches are used in interspecific signaling, such as the aposematism seen in black and white mephitids and porcupines.

Coloration has consequences for heat management, and also for UV protection, most famously skin coloration in humans.

We attempt to integrate developmental and evolutionary approaches to explain the origins of mammalian coloration.

## The Diversity of Mammalian Color Patterns

Zebras became striped after 'standing half in the shade and half out of it, and what with the slippery-slidy shadows of the trees falling on them' [1].

Although children learn the striking colors of mammals from an early age, that (zebras *Equus* sp.) are striped, leopards (*Panthera pardus*) are spotted, and giant pandas (*Ailuropoda melanoleuca*) are black and white, they are still kept in the dark as to how and why these coloration patterns arise, shielded from science through fairy stories. Yet, we now know an increasing amount about the development and function of mammalian coloration. Here, we summarize genetic and developmental mechanisms underlying these phenotypes. Second, we review the functions of mammalian external appearances, a group in which crypsis predominates but where **signaling** (see Glossary) to conspecifics and to predators occasionally prevails. Finally, we suggest ways in which these approaches can be consolidated.

## Genetics of Hair Pigmentation: Historical Perspective

Beginning in the 18th century China and Japan, so-called mouse fanciers collected, maintained, and bred together unusual color morphs of wild mice [2]; in doing so, these amateur geneticists generated mouse strains with distinct color variation. Thus, pigmentation phenotypes in mice, and later rats and guinea pigs, were readily available for study. Coat-color phenotypes were used as early as the 1900s to test several fundamental concepts in genetics – from Mendelian inheritance [3,4] to linkage [5], to demonstrations of epistasis and pleiotropy [6].

Because of the utility of pigment phenotypes, a sizeable list of genetic loci with well characterized phenotypes has since accumulated. The first pigmentation gene to be cloned, tyrosinase-related-protein-1 (*Tyrp1*), was initially thought to be the gene responsible for **albinism**, but was later mapped, cloned, sequenced and correctly attributed to the tyrosinase locus [7,8]. Since then, more than 100 genes affecting pigmentation have been cloned in mice and it is likely that many more remain to be identified [9] with ongoing chemical mutagenesis programs (Mouse Genome Database).

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## Pigmentation Regulation and Patterning

Color variation in mammals is primarily determined by two factors: (i) pigment regulation, altering the type, density and/or distribution of pigments along individual hairs; or (ii) pigment patterning, altering the spatial distribution of pigmentation across the body. Both of these processes can have profound effects on overall appearance, but likely have a distinct genetic basis and are manifested in different parts of the developmental pathway.

Pigment regulation: mammalian hair color results from a complex process involving the migration, differentiation, and regulation of melanocytes, the pigment producing cells in the epidermis [10]. Melanocytes can produce two types of melanin pigment, **eumelanin** and **pheomelanin**, through a process that is primarily determined by the interaction between *Agouti* and α-melanocyte stimulating hormone (MSH) with the melanocortin-1 receptor (*Mc1r*) [11]. When *Agouti* is not present, α-MSH will readily bind to *Mc1r*, causing intracellular cAMP to accumulate inside the cell. cAMP accumulation leads to the downstream activation of *Tyr* and the eventual production of eumelanin. When *Agouti* is present, it binds to *Mc1r* and causes a decrease in the production of intracellular cAMP, which eventually leads to downregulation of *Tyr* and causes melanocytes to switch from the production of eumelanin to pheomelanin [11]. Genomic changes in *Agouti/Mc1r* as well as in the genes involved in the downstream enzymatic reactions governing melanin synthesis underlie natural variation in mammalian coats [12].

Pigment patterning: in vertebrates, several mechanisms may contribute to regional variation in melanin type, density, and distribution. During embryogenesis, neural crest cells differentiate into melanoblasts (precursors of melanocytes) that migrate ventrally along the body axis. Melanoblasts typically enter the epidermis, where some remain (in certain species), while others localize to the hair follicles and differentiate into melanocytes. Once mature, these melanocytes can produce pigment, which is then packaged into melanosomes and transferred to keratinocytes of developing hair [13].

Pigment patterns can be classified as random and nonrandom, based on developmental origin and appearance [12]. Random patterns, such as those seen in some breeds of domestic animals, arise from stochastic developmental events affecting melanocyte behavior. For example, the white-spotting phenotype commonly present in cats and dogs is caused by a failure of melanocyte migration. In contrast, nonrandom patterns, such as periodic stripes and spots, arise from spatially constrained developmental processes. Recent advances in genomics show how molecular mechanisms shape natural variation in mammalian pigment patterns. Although *Agouti* plays a central role in regulating melanocyte behavior during hair growth (see above), a different isoform of *Agouti* is expressed during development and can directly influence melanocyte maturation. In *Peromyscus* mice, differences in the position of the dorsal/ventral pigmentation boundary, seen in two locally camouflaged populations, are explained by changes in the spatial expression domain of *Agouti* that occur during embryonic development [14]. This example illustrates how the same gene, through the production of different isoforms, can influence pigmentation patterning (ventral-specific expression during development) and pigment distribution within a single hair (switch from eumelanin to phaeomelanin production). In African striped mice, *Rhabdomys pumilio,* which have a coat comprised of dark and light longitudinal stripes (Figure 1A), the transcription factor ALX3 is expressed at high levels in the light stripes where it acts to repress melanocyte differentiation and pigment production [15]. Kaelin and coworkers [16] used a combination of association and gene expression studies to show that periodic patterns (spots and stripes) in felids are established in two stages: first, when skin is developing, the gene *Taqpep* is involved in setting a prepattern that is later implemented during hair growth by the gene *Edn3*; a secreted factor that is expressed at high levels in the black spots of cheetahs (*Acinonyx jubatus*),

### Glossary

**Albinism:** a genetic condition that reduces the amount of melanin formed in the skin, hair, and/or eyes.
**Dichromat:** possesses two independent channels for conveying color information, derived from the two different types of cone cells in the eye.
**Diurnality:** being active during the day.
**Eumelanin:** the other type of melanin produced by melanocytes in mammals. Eumelanin is largely responsible for black/brown hair.
**Introgression:** transfer of genetic material between hybridizing species.
**Pelage:** the fur, hair, or wool of a mammal.
**Pheomelanin:** one of the two types of melanin produced by melanocytes in mammals. Pheomelanin is largely responsible for red/yellow hair.
**Signals:** are acts or structures produced by signalers , which have evolved for the purpose of conveying information to recipients, such that the information elicits a response in recipients resulting in fitness consequences that, on average, are positive for both the signaler and recipient.
**Trichromat:** possesses three independent channels for conveying color information, derived from the three different types of cone cells in the eye.

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Figure 1. Selected Species of Mammals That Are Currently Being Used to Further Understanding of Developmental[a] and Evolutionary[b] Mechanisms Driving Coloration in Mammals. Top left: African striped grass mouse *Lemniscomys pumilio*[a]; top right: snowshoe hare *Lepus americanus*[a,b]; middle left: oldfield mouse *Peromyscus polionotus* [a,b]; middle right: Preuss's guenon *Cercopithecus preussi*[b]; bottom left: plains zebra *Equus quagga*[b]; bottom right: melanistic gray squirrel *Sciurus carolinensis*[a] (photographs from WikiMedia).

where it promotes melanocyte differentiation and proliferation. These three examples demonstrate how specific genes, by being expressed in a spatially restricted fashion, can act to establish color differences along the body. Remarkably, spatially restricted gene expression patterns can also be seen at much smaller scales, such as within a single hair follicle: in Dun horses, *Equus ferus*, the transcription factor TBX3 is expressed only in the posterior half of hair follicles, resulting in radially asymmetric deposition of pigment in hair follicles [17].

## Introgression as a Source of Color Variation

Although differences in color between and within individuals can be generated via changes in the coding sequence of genes or the regulatory region of genes controlling pigment synthesis or pigment patterning, it is becoming more evident through the use of genomic and molecular approaches that factors other than mutations, such as **introgression**, play a major role in promoting color variation in mammals. For instance, melanism in North American gray wolves, *Canis lupus*, is caused by a mutation in the *K* locus, which encodes a β-defensin protein that acts as an alternative ligand for

*Mc1r*. By analyzing the evolutionary history of the melanistic *K* locus, Anderson and colleagues [18] were able to determine that this mutation, which has risen to high frequency and displays signatures of positive selection, originated in domesticated dogs and was transferred to wolves through past hybridization events. Thus, a mutation originally selected in a domesticated animal has provided favorable genetic diversity in a natural population. In another example, southern populations of snowshoe hares, *Lepus americanus*, no longer moult from a brown to a white coat in winter, like their northern counterparts (Figure 1B), but remain brown all year. As southern populations experience milder winters with less snow, brown coats allow them to better blend in with the environment and avoid predator attack. Using association mapping and population genetic analyses, Jones and colleagues [19] showed that this variation maps to a regulatory region in the gene *Agouti*, and that the brown winter coat allele was likely introgressed from black-tailed jackrabbits (*Lepus californicus*). Thus, introgression has provided snowshoe hares a key source of genetic variation to adapt to rapidly changing environments. In another recent study, McRobie and coworkers [20] found that melanism in gray (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) is caused by the same amino acid change in *Mc1r*, and that this allele likely originated in fox squirrels and introgressed into gray squirrels. Each example illustrates the importance of introgression as a continuous source of genetic variation upon which natural selection can act.

## Color Change in Mammals

Despite the fact that hair color is largely determined by the genotype of an individual, mammal **pelage** color is not necessarily fixed throughout the lifetime. Some changes are age-related: certain suids, felids, and artiodactyls, for instance, are born with spotted or striped coats that become uniform when offspring become mobile. In pigs and peccaries, variegated pelage is associated with litter size perhaps because neonate interactions attract predator attention [21], whereas in felids and artiodactyls young are sequestered in hidden locations. Some pinniped and primate species are born with natal coats, which neonates soon lose. Although we know that white seal pups match a snowy white arctic background, or are dark if born in caves or on predator-free islands [22], the functions of black, white, orange, or gray neonate pelage in primates remain elusive but include attraction of allomothers and reduction of infanticide by males. Hair color may also change in old age as in the silvery white of human hair. Second, a few mammals change color seasonally, such as ermines (*Mustela erminea*) and snowshoe hares, to match a white arctic background in winter, and later to match background soil in spring, a cycle that is being disrupted by climate change [23].

Turning from crypsis to intraspecific signals, mammalian pelage color may vary according to dominance, as in males from uni-male units turning dark blue–black in the greater kudu (*Tragelaphus strepsiceros*) or ashen in mountain gorillas (*Gorilla beringei*). Finally, skin color can change rapidly due to hormones and vasodilation, particularly in primates. For example, tumescent red genitalia may advertise fertility and possibly ability to raise offspring to independence in female baboons (*Papio cynocephalus*) [24], and may be used in mate choice in rhesus macaques (*Macaca mulatta*) [25]. Male genital hue or facial luminance can signal dominance, as in vervet monkeys (*Chlorocebus pygerythrus*) or mandrills (*Mandrillus sphinx*), respectively [26–28]. Even more rapid signaling is possible: changing blood supply can alter facial coloration in response to anger or stress. Blushing in humans may be such an example, although surprisingly little work has been conducted since Charles Darwin devoted a chapter to it in his 1872 book, the *Expressions of Emotions in Man and Animals* [29].

## Color Vision

Knowledge of species' and individuals' differing spectral sensitivities might help us understand the role that external color appearances play in interspecific and intraspecific signaling. Mammals

were originally thought to be **trichromats** based on their reptilian ancestry but evolved to be **dichromats** with maximal retinal sensitivities in short and medium wavelengths of the visual spectrum when they became nocturnal, so *a priori*, they might be expected to be dowdy. However, some primates and perhaps a few marsupial species secondarily became trichromats coincident with the advent of **diurnality** [30]. The evolution of routine trichromacy (see below) in African and Asian monkeys and apes [30] may have been driven by the benefits of picking out orange and red ripe fruits and edible young leaves from a background of mature green leaves [31–33] but the relationship between vision and foraging benefits is complex [34,35]. Reconstructions of the ancestral states under maximum parsimony indicate that trichromatic color vision evolved at the ancestor to extant tarsiidae–platyrrhine–catarrhine species before the evolution of red skin or pelage, suggesting that the presence of color vision may have been necessary for the evolution of red external appearance in primates [36] but the association is not strong [37].

Among catarrhine primates, both sexes discern hues in the red–green range and along the ancestral blue–yellow color axis [38]. This routine trichromacy is enabled by two distinct opsin genes on the X chromosome that code for mid-wavelength-sensitive (MWS, green) and long-wavelength-sensitive (LWS, red) cone photopigments, and a third autosomal opsin gene coding for short-wavelength-sensitive (SWS, blue) pigments. In contrast, certain lemurs and most primate species from the Americas possess polymorphic trichromacy due to allelic variation of a single mid- to long-wavelength-sensitive opsin gene (M/LWS). In these polymorphic species, some females and all males are red–green color blind, and only females that are M/ LWS heterozygotes are capable of trichromatic vision [38–40]. Howler monkeys (*Alouatta* sp.), however, are an exception and have independently evolved routine trichromacy similar to catarrhines; interestingly, they are heavily reliant on young red leaves [41].

Whether trichromatic species are more colorful than dichromats is little researched but at present the association seems weak [37]. A related proposal with stronger support is that medium- and long-wave cone maximum sensitivities for trichromats are optimized for discriminating variations in blood oxygen saturation so that trichromacy may also be linked to primate facial and sexual skin coloration as found in Asian and African groups [28,42].

## Evolutionary Drivers: Crypsis

Rodents and bats, constituting approximately one quarter and one fifth of mammals respectively, are often dull browns or grays probably to match their background to avoid detection. Research on rodent hair color has a long history with early North American mammologists such as Sumner, Benson, Dice, and Blossom describing coat color variation in US southwestern desert rodents [43]. For example, they showed that in the rock pocket mouse (*Chaetodipus intermedius*), coat color typically matches that of rubble on which the mice live; the dorsal pelage varies from a light, sandy color for populations found on some granites to dark, nearly black for populations found on basalt lava flows. These pelage hues, in some cases stemming from *Mc1r* mutations [44], are likely selected for by owl predation [45,46] with patterns of migration across different substrates driven by stronger selection against light morphs on a dark background than against dark morphs on light background [47] (Figure 1C). Phenotype–environment matches also occur on much larger geographic scales [48], while interspecific comparisons of other small mammalian prey species similarly indicate pelage coloration matches different backgrounds [49]. Background matching is the form of protective coloration whose genetic basis is best understood.

Of course, it is not just prey that need to remain cryptic. Carnivores need to approach prey unnoticed; think of white polar bears (*Ursus maritimus*) approaching seals hauled out on ice. Other carnivores and perhaps pinniped and cetacean piscivores wear spotted, dappled, or uniform fur to

approach their prey undetected; ocelots (*Leopardus pardalis*) and tigers (*Panthera tigris*) on land [50], gray seals (*Halichoerus grypus*) [22], and Atlantic spotted dolphins (*Stenella frontalis*) [51] at sea are all examples of what used to be called aggressive coloration in Victorian times.

Beyond background matching, many mammalian prey are countershaded (dark on top, lighter underneath). This pattern is common in both terrestrial and aquatic animals although the underlying mechanisms are hotly debated and include crypsis, protection from UV light, and reducing abrasion [52]. In some mammals, the dark to light boundary on the animal's lateral surface precisely counteracts the shadow cast by the animal's own body [53] perhaps rendering it 2D and thus more difficult to detect than a 3D object. However, there must be other influences on dorsal pigmentary darkening: the white ventrum of murids hugging the ground is unlikely to have evolved for the same reasons as a gerenuk (*Litocranius walleri*) with its long legs. Other mechanisms of remaining cryptic through disruptive coloration, masquerade or transparency have yet to be identified in mammals.

## Evolutionary Drivers: Signaling

Many aspects of coloration in birds are driven by male–male competition and female choice but these evolutionary drivers seem to have less force in mammals, except perhaps in African and Asian primates where ornamental skin patches are more common [54] and in gibbon species where males and females differ in pelage color. Sexual differentiation in fur color is also found in a tiny handful of other species such as the male ribbon seal's (*Histriophoca fasciata*) red inflatable nostril, the mouflon's (*Ovis orientalis*) blond beard, and various dark male bovids and pinnipeds but has received minimal study [55]. The best worked example is the black manes of lions (*Panthera leo*) that are attractive to females but intimidating to other males [56], a male ornament kept in check by overheating.

Color patches are used in *interspecific* signaling; the most famous being aposematic coloration in mustelids that advertises noxious anal secretions [57]. However, contrasting color patches can be used to thwart predators in other ways. Black flank stripes of gazelles amplify pursuit deterrent stotting behavior [58], and conspicuous ear tips of lagomorphs may deter pursuit [59]. Some color regions such as white heads in cetaceans may function to drive fish into shoals for easier capture [51]. Complex primate face colors may signal species' identity so as to avoid hybridization in sympatric primate congeners [60,61] (Figure 1D). It is challenging for researchers to explain the absence of sexual dichromatism in mammals where mate choice is common, or the anachronistic distribution of color patches used in signaling to other species [62].

Perhaps the take home message is that there is no single evolutionary cause of conspicuous pelage in mammals [63]. Black and white coats of zebras are not a form of warning coloration (Figure 1E): instead a growing number of studies indicate that stripes thwart attack by disease-carrying biting flies [64–66]. In giant pandas, comparative work indicates white fur blends in with background snow, black legs with deep forest shade, but black eyes spots and ears help in individual recognition and signal aggressive intent [67]. Blackbuck (*Antilope cervicapra*) are sharply countershaded (black above, white below) to counteract dark shadow cast by the glaring tropical sun [53], while the functional significance of black and white coats of colobus species, Malayan tapirs (*Tapirus indicus*) and orcas (*Orcinus orca*) are still enigmatic but likely to differ from each other.

## Evolutionary Drivers: Physiology

From first principles, we assume that external coloration has inevitable consequences for heat load; lighter coats reflect heat and are found in deserts, for instance. However, we still know little

about the relative contributions that hair color, density, length, and structure contribute to temperature regulation in mammals. Like several other groups, mammals are darker in the tropics (Gloger's rule) but the melanin that produces darker color has other consequences including being relatively impervious to abrasion, antimicrobial benefits, preventing UV-caused mutagenesis, and absorbing heat, so that the underlying mechanisms for Gloger's rule may be multifaceted [68,69]. In an important study, Hetem and coworkers [70] implanted thermodevices in three differently colored springbok (*Antidorcas marsupialis*); a species that is normally light brown in color although black and white morphs exist. Daily maximum temperatures of the black morph were significantly higher than normal or white morphs in spring due to absorbing more solar radiation. Daily minimum temperatures in the winter were significantly lower for the white than the black or normal morphs. Thus, stabilizing selection appears to act at different periods over the year. In winter, black morphs reduce energy expenditure but experience higher heat load in summer. White morphs live close to the energetic edge in winter. The normal springbok occupies a compromise position which may explain why few black and white morphs are found. Oddly, the relationship between hair color and thermoregulation is little explored in other mammals.

Turning to UV radiation protection, humans are polymorphic for skin color with people living at higher latitudes having lighter skin than those nearer the tropics where UV radiation is stronger. The underlying principles are well established and often used as an example of evolutionary trade-offs in teaching students about evolution. On the one hand, eumelanin prevents UV from causing oxidative damage to DNA which can result in skin cancer. Additionally, it prevents vitamin B folate photolysis. Folic acid is an essential nutrient needed in nucleotides and hence DNA synthesis, especially in maturing bone marrow and developing red blood cells. Exposure to excessive amounts of UV leads to folate deficiency and this results in fetal abnormalities especially spina bifida and anencephalitis where the neural tube fails to close properly in the developing embryo. On the other hand, UV promotes the synthesis of Vitamin D3 in the skin. Vitamin D has many positive effects including promoting bone formation and mineralization and reducing cardiovascular disease, diabetes, multiple sclerosis, and inflammatory bowel disease. While there is sufficient UV at lower latitudes for people to synthesize vitamin D, even with melanized skin, there is not enough UV at higher latitudes so people must reduce melanin synthesis and consequently have lighter skin. Humans living in intermediate latitudes (in the Mediterranean) with high annual variance in UV show facultative tanning in which melanization starts slowly allowing vitamin D production to occur in spring and winter, but prevention of vitamin B folate photolysis in hot summer months [71,72].

In addition to the physiological impacts of differences in color described above, it is worth noting that the physiology of an organism can have a large impact on color production, mediated by hormones. For example, melatonin and prolactin play a key role in regulating seasonal moulting in various animals: when days get shorter, specialized photosensitive ganglion cells in the eye retina convey a signal that ultimately reaches the pineal gland, which controls secretion of melatonin. Melatonin is produced at night at rates that are inversely proportional to day length. During the winter, as days get shorter, higher levels of melatonin inhibit the production of prolactin, leading to the production of white winter fur [73].

## Concluding Remarks and Future Perspectives

At present, the study of mammalian coloration is divided into two camps – developmental and evolutionary – that, with notable exceptions [14,74–76], interact infrequently (hence our attempt here). Developmental biologists concentrate on cellular mechanisms and morphology, whereas evolutionary ecologists focus on behavioral and ecological variables to explain macroevolutionary patterns. Moreover, the former relies on model systems of a handful of species whereas the latter

### Outstanding Questions

Can developmental biologists take advantage of recent advances in genomic and molecular approaches to study the mechanisms underlying natural variation in mammalian pigment patterns?

Can we incorporate mechanistic studies of color/color pattern formation into a comparative phylogenetic context so that we can understand whether convergent phenotypes have arisen through similar molecular mechanisms?

What factors constrain the evolution of conspicuous skin coloration in primates?

Why do some primates have distinctive natal coat coloration?

Why does conspicuous coloration evolve in mammals that are not aposematic?

Why is sexual dichromatism so rare in mammals?

What are the mechanisms underlying Gloger's rule in mammals?

often focuses on many species in a clade. We see three ways to bridge this divide (see Outstanding Questions). First, we need to test the ecological significance of phenotypes being studied at the molecular level. Already experimental and observational studies show that different selective backgrounds drive population gene frequencies [76]; that the relative strengths of selection on alleles that code for pelage background matching differ according to habitat [77]; and that changing ecology can precede changes in genetic variation [78]. However, although we understand that the terminal differentiation of ventral melanocytes is delayed in mice that are countershaded as adults [14], we do not understand the adaptive significance of countershading in rodents. Similarly, we understand the genetic underpinnings (*ALX3*) of striping in striped mice species [15] but not its adaptive significance. Moreover, we have yet to make genetic modifications in known pigmentation/patterning genes and then test their effects on survival and reproduction in the wild. This is now within our grasp since we have the capability to manipulate genomes of a diversity of species [79,80].

Second but conversely, we need to understand the molecular and developmental basis of phenotypes that have already been shown to be adaptive. We can already do this for melanin in humans and some rodents in fire climax populations [81,82]. For example, the *MC1RΔ24* allele is associated with melanism in both gray squirrels and fox squirrels [20]. However, there are other advantages of melanism for species living in shady or humid dark environments [83,84] (Figure 1F) that could be explored genetically. We are still a long way from knowing the molecular underpinnings of say aposematism or primate skin and hair color.

Third, we need to combine evolutionary and developmental approaches to understand convergence. For instance, the repeated appearance of pigment patterns and color morphs is key to evo-devo biology and we need to map developmental mechanisms underlying pelage coloration onto a phylogenetic tree to confirm that these mechanisms are conserved across the mammalian clade. And while we are getting a good handle on simple whole body changes in color from both genetic/developmental and ecological standpoints, we do not know if the rules governing mechanisms and functions are congruent across species. Once we can marry these disciplines the study of mammalian coloration will take a large step towards reaching maturity [85].

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