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Review

The colours of extant mammals

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ABSTRACT

In this review I survey pelage and skin colouration patterns of the 29 orders of extant mammals and assess their functional significance. The vast majority of mammals are shades of grey or brown. Concealment is probably the principal evolutionary driver of pelage colouration in this Class likely through background matching and self-shadow concealment. A small minority of species are aposematic while many others have distinctive markings used in intraspecific and interspecific communication although the meaning of these markings is unclear. Colouration in mammals also has physiological consequences but these are barely understood as yet.

Contents

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1. Introduction

Pelage and skin colouration in mammals is driven by three broad evolutionary forces: concealment from predators or prey, communication within or between species, and diverse physiological considerations [1]. Concealment in mammals may arise in several ways: through background matching where the animal's appearance generally matches the colour, lightness and pattern of one or several background types [2,3], or through self-shadow concealment where directional light which would lead to the creation of shadows is cancelled out by countershading usually through dorsal pigmentary darkening [2,4]. Concealment may also be mediated through obliterative shading where countershading leads to the obliteration of three-dimensional form [2], or through disruptive colouration where a set of markings creates the appearance of false edges and boundaries, and hinders the detection of an object's, or part of an object's, true outline and shape [2,5], or even through masquerade where recognition is prevented by resembling an uninteresting object, such as a leaf or stick [2]. Communication may be between rivals, mates or family members; or it can be between different species in competitive interactions or for conveying information to would-be predators [6]. Physiological concerns include thermoregulation [7]. Mammals' external colouration derives from body fur colour in terrestrial and amphibious mammals as well as the hair colour of eartufts, moustaches, manes and tail-tips in some species. External colouration also derives from skin colour in aquatic mammals, and from tails, faces and genitals of some terrestrial species, sometimes driven by sexual selection in the last two instances.

Yet despite several ways of modifying external appearance, colouration in mammals is regarded as being less striking than in other vertebrates. Why is this? One possibility is that most mammals have dichromatic vision which may reduce the importance of colouration in concealment and communication [8]. Another is that most mammals are active at night when lighting conditions are poor although the moon is not an insignificant source of light [9]. A third is that the mechanisms through which hair colour is produced are limited: only eumelanin and phaeomelanin are deposited in hair shafts [10]. The former pigment is responsible for black and brown colouration whereas phaeomelanins are reddish-brown pigments that predominate in red and yellow fur. Another type of colouration, agouti, is produced by alternating eumelanin and phaeomelanin banding in hairs. If reddish bands are reduced in number across species or within an individual's lifetime, pelage transforms from agouti to dark brown or black. With further depigmentation it leads to grey, silvery, creamy or eventually colourless hair. If black bands are lost, however, pelage transforms from agouti to reddish-brown and with further depigmentation to orange, gold, straw, and cream to colourless [11].

In skin, melanocytes are responsible for the synthesis of melanins in membrane-bound melanosomes and their transport to epidermal cells. Melanin absorbs many wavelengths of light which protect the skin from ultraviolet light; melanin is also an antioxidant, can sequester harmful trace elements, strengthen tissue, has antimicrobial properties, and may aid in thermoregulation [12]. Skin colouration in mammals is further affected both by carotenoid pigments (that cannot be manufactured by vertebrates and can therefore reflect foraging history) and blood circulating through capillaries (that can thus signal anaemia). Red and yellow epidermal colouration may therefore signal body condition.

Although colouration in mammals is under these mechanistic constraints, coat colour can in some species change during ontogeny or seasonally, some species are polymorphic, some are sexually dichromatic, and most show considerable intraspecific variation in pelage colour; some species even apply cosmetic colouration from soil. Therefore the diversity of mammalian colour forms is more varied than commonly assumed and demands explanation. Here I review the breadth of colouration patterns in all 29 orders of extant mammals [13,14], summarize existing functional explanations, and point to the numerous gaps that remain in our understanding of the evolution of external appearance of mammals.

2. The mammalian orders

2.1. Monotremata

All four echidna species have short spines on their lateral and dorsal surfaces that are white, light brown or have black and white bands. Predators find it difficult to handle or kill echidnas especially if they are lodged in borrows or crevices suggesting that their colouration is aposematic [15]. The duck-billed platypus *Ornithorhynchus anatinus* has light brown fur.

2.2. Didelphimorphia

Colouration in marsupials is very poorly studied so that functional explanations for pelage colouration are anecdotal. Most of the 92 species (numbers are approximate throughout) of American opossums have dark or light grey fur or brown or golden pelage. Some of the Didelphidae have facial masks including the grey four-eyed opossum *Philander opossum* with white spots above its eyes, or have eye masks such as the Mexican mouse possum *Marmosa mexicana*, or else have black and white faces; the functions of these markings are unknown. Other species have swathes of black or white fur covering shoulders or ventrum perhaps for intra- or intersexual signalling. Some marsupial species have trichromatic vision [16] and the scrota of some species, such as the long-furred woolly mouse opossum *Micoureus demerarae*, are azure and possibly signal dominance.

2.3. Paucituberculata

The six caenolestid species are small nocturnal marsupials that inhabit a variety of altitudes in western South America. They are dark grey presumably for background matching, some with banded rat-like tails, but little is known of their biology.

2.4. Microbiotheria

The monito del monte *Dromiciops gliroides* is a small monotypic member of this order living in dense humid forests of Chile and Argentina. It has a grey-brown dorsum turning lighter on its lateral surfaces with a white belly (countershading that might reduce