The Adaptive Significance of Coloration in Mammals

The Adaptive Significance of Coloration in Mammals

TIM CARO

Coloration is a diagnostic tool for identifying mammals, but inquiry into its function has lain dormant for almost a century. Recently, the topic has been revived and modern phylogenetic methods have been applied to large data sets, allowing researchers to assess, for the first time, the relative importance of three classic hypotheses for the function of coloration in mammals: concealment, communication, and regulation of physiological processes. Camouflage appears to be the single most important evolutionary force in explaining overall coloration in mammals, whereas patches of colored fur are used for intraspecific signaling. Sexual selection is associated with flamboyant ornamentation in a minority of primates and other restricted mammalian taxa, but to a far lesser extent than in birds. Interspecific signaling among mammals includes aposematic coloration, exaggeration of signals to deter pursuit, and lures for misdirecting predatory attack. Physiological causes of coloration, including melanism, are evident but poorly researched. The relative importance of evolutionary forces responsible for external coloration varies greatly between vertebrate taxa, but the reasons for this variation are not yet understood.

Keywords: comparative method, color, functional hypotheses, mammals, signals

One of the first things children learn about nature is that certain large mammals have characteristic fur colors: The giraffe is reticulated (i.e., its reddish-brown coat is divided by a network of fine white lines into large geometric shapes), whereas the skunk and giant panda are black and white (figure 1a). When children ask why, adults recite reasons that were formulated more than a century ago, when naturalists speculated about the survival value of pelage and skin colors that they saw in specimens brought back from collecting expeditions (Wallace 1889, Poulton 1890). Parents' dated or incomplete answers (camouflage, advertisement, or "I don't know") stem not from their own ignorance but, sadly, from the fact that the field has advanced so little in 100 years. Naturalists' anecdotes about mammalian coloration were never put to experimental test, and the generality of these ideas—most of them formulated on the basis of only one or a handful of species—remained unexplored until very recently, except for one monumental treatise (Cott 1940). Now, however, we are in a better position to answer children's awkward questions with a modicum of authority.

The most salient point about the evolution of animal coloration is that different species and different parts of the body are subject to different selective pressures (Hingston 1933, Cott 1940). Classically, these can be divided into concealment, communication, and regulation of physiological processes.

My purpose here is to review new evidence for each of these evolutionary pressures that may have helped to form skin and pelage coloration in mammals and to attempt to assess their relative frequency in nature.

Concealment

Animals can remain concealed when their overall coloration (box 1) resembles or matches the natural background of their environment (Endler 1978). This phenomenon, also known as *general color resemblance,* includes crypsis (a type of camouflage), in which overall body color resembles the general color of the habitat, or pattern blending, in which color patterns on the body match patterns of light and dark in the environment. Background matching may change seasonally (termed *variable background matching*) or with age. Concealment may also be achieved through disruptive coloration (also termed *obliterative shading*) by contrasting colors or irregular marks that break up the body's outline (Merilaita 1998). Finally, animals may attain concealment if they have a lighter ventral surface, because this may counteract the sun's effects—lightening the dorsum and shading the ventrum—when it shines from above (Thayer 1909, Kiltie 1988).

Uniform coloration. There is overwhelming evidence of mammals' pelage coloration matching their backgrounds, both between and within species. Across species, at least five different coat colors appear to match the typical background on which they are found among carnivores, artiodactyls, and

Tim Caro (e-mail: tmcaro@ucdavis.edu) is a professor in the Department of Wildlife, Fish and Conservation Biology and the Center for Population Biology, University of California, Davis, CA 95616; he conducts research on antipredator defenses and conservation of tropical ecosystems. © 2005 American Institute of Biological Sciences.
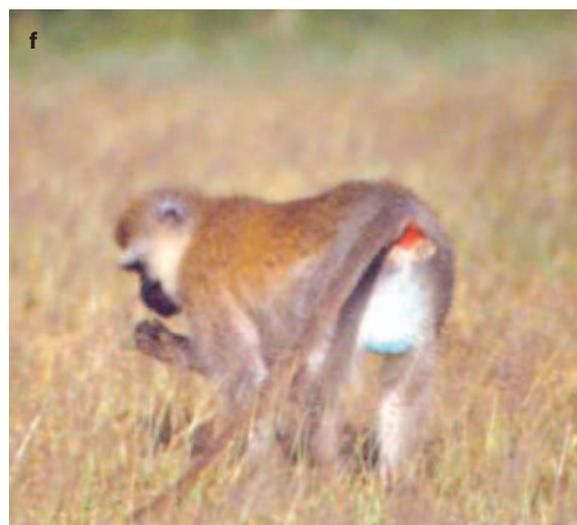
Figure 1. Striking examples of mammalian coloration: (a) striped skunk (photograph: © 1989 Jeff Wilcox, used with permission), (b) Burchell's zebra (photograph: Tim Caro), (c) ermine (photograph from the collection of the Museum of Wildlife and Fish Biology, University of California–Davis, used with permission), (d) tiger (photograph: Tim Caro), (e) beisa oryx (photograph: Tim Caro), and (f) vervet monkey (photograph: © 1987 Lynne Isbell, used with permission).

Box 1. The measurement of color.

The artist Albert Munsell developed a system for measuring color. He divided hue into 10 classes, red, yellow, green, blue, purple, and their intermediates; he then divided saturation, also known as chroma or intensity, into 6 uniform steps from 0 to 5; finally, he divided tone, or brightness, into 10 intervals ranging from black (0) to white (10). These scores can be measured using a reflectance spectrophotometer, or they can be compared to color chips in a standard reference collection. This has become standard practice in avian studies (Hill 2002), but it is rarely used for mammals (but see Sumner and Mollon 2003). Instead, color is still scored subjectively, classifying first the overall coloration of the coat as patterned or uniform (usually ignoring variation, e.g., lumping black, dark brown, dark gray-black, and brown-black under "dark") and then the markings on specific body parts, usually extremities, such as ears, tails and legs. Markings are defined as an area of color contrasting with the rest of the body or with the nearest area of the body. Thus, a white tail tip on a white animal would not be recorded as such, but a white tail tip on a black animal or one with a black tail would constitute a marking (Ortolani and Caro 1996).

Unfortunately, for most taxa, it is difficult to relate coloration or markings to crypsis (camouflage) or conspicuousness because animals that are easy to notice close up may be difficult to see a long way off; zebras are highly conspicuous nearby but surprisingly difficult to see at a distance (figure 1b). Second, the contrast between an animal and its background depends on ambient illumination and spectral reflectance to the background; thus, an animal may be cryptic at one time of day but not later on (Burtt 1981), or against one background but not another (Endler 1990). Third, an animal may be conspicuous to humans but not to nonprimate animals, because primates have three types of color-sensitive retinal cones, whereas carnivore predators possess only two; or they may be cryptic to humans but conspicuous to birds, which have four types of cones, the additional one of which is sensitive to ultraviolet light. Most mammalian studies throw caution to the wind and assume that the human visible spectrum is representative of all the visible spectra possessed by conspecifics and predators in an animal's environment.

lagomorphs, the three orders in which statistically and phylogenetically controlled comparisons have been made to date (table 1). Thus, species that are white or become white in winter are found in arctic and tundra biomes (figure 1c), pale species in desert and open environments, red and gray species in rocky habitats, and dark species in closed environments and in dense or tropical forests. Unfortunately, these robust associations do not make a clear-cut case for concealment, because coats of different color have differing thermoregulatory properties. White fur might scatter solar radiation toward the skin and hence be expected in cold climes; pale fur that reflects light might be expected in very hot environments such as deserts; and dark fur might be expected in the tropics, because it enhances water evaporation more readily than cool surfaces (Gloger 1833) or because it protects against ultraviolet radiation.

The same findings pertain within species. Individual desert rodents with paler coats are found on pale soils, and those with darker coats are found on blackened lava beds (Belk and Smith 1996), but again, vigorous argument has raged over whether the close match signifies camouflage or thermoregulation, with experimental studies on predation by owls eventually tipping the consensus in favor of protective concealment (Kaufman 1974). In a handful of species, individuals are polymorphic for coat color (see box 2).

Pattern blending. Less equivocal evidence of background matching that acts as concealment comes from pattern blending. A coat with the appearance of dappled light, for exam-

ple, might be expected in a diurnal, solitary species that lives in forests, where crypsis is a likely mechanism by which an animal could escape notice. This has been confirmed in artiodactyls (table 2); in particular, there is a very tight association between young having spotted coats and young being sequestered during the first week after birth (hider species; figure 2). Among carnivores, spotted species tend to be arboreal and to live in closed habitats, whereas striped species are found in grasslands, supporting the hunters' old adage that tigers are striped to hide in tall reeds and grasses (figure 1d).

Disruptive coloration. It is difficult to marshal convincing evidence for disruptive coloration in mammals. Numerous artiodactyls have prominent black side bands and leg markings that could function to break up the body's outline; but although these markings are found in species that are diurnal and live in open country and in desert habitats, few associations between potentially disruptive coloration and these behavioral and ecological variables stand after controlling for phylogeny (Stoner et al. 2003a). Black-and-white species such as giant anteaters, tapirs, and giant pandas, obvious candidates for disruptive coloration, will require difficult experimental approaches; being found in orders with so few other black-and-white species, they defy comparative analyses.

Self-shadow concealment. Countershading is widespread in mammals, and one function may be to aid in concealment by reducing shadow in well-lit environments. For example,

Table 1. Summary of significance tests showing relationships between the overall uniform coloration of different mammals (artiodactyls, carnivores, and lagomorphs) and types of habitat.

	Habitat associated with animal color				
Group	**White**	**Pale**	**Red**	**Gray**	**Dark**
Artiodactyla	Arctic*[a], tundra‡[a]	Open environment*, desert*	NS	Rocky*	Tropics‡, closed environment*, dense forest*
Cervids	Arctic‡[a], tundra‡[a]	NS	NS	NS	Dense forest*
Bovids	Arctic‡[a], tundra‡[a]	Open environment*, desert*	Not rocky*	Rocky*	Tropics‡, closed environment*, dense forest*, swamp*
Carnivora	Arctic‡[b]	Desert‡	NT	NT	Tropical forest‡
Canids	Arctic‡[b]	Desert‡	NT	NT	Tropical forest‡
Ursids	NS	NA	NT	NT	Tropical forest‡
Procyonids	NA	NA	NT	NT	NS
Mustelids	Arctic‡[b]	NA	NT	NT	NS
Viverrids	NA	NA	NT	NT	NS
Herpestids	NA	NA	NT	NT	Tropical forest‡
Hyaenids	NA	NA	NT	NT	NA
Felids	NA	NS	NT	NT	NS
Lagomorpha	Arctic*[a], tundra*[a]	Open environment‡, desert‡	Rocky‡	Rocky*	Forest/woodland*

Asterisk (*), significant results of nonparametric chi-square or Fisher exact probability tests; ‡, significant results of phylogenetically controlled comparisons using MacClade and Maddison's concentrated changes tests (Maddison 1990).

NA, not applicable (no species showing that type of coloration); NS, not significant (no significant association found between coloration and habitat); NT, not tested.

a. Includes only species that turn white in winter, not species that remain white all year.
b. Includes species that turn white in winter and species that remain white all year.

Source: Ortolani and Caro 1996, Ortolani 1999, Stoner et al. 2003a, 2003b.

Table 2. Summary of significance tests showing relationships between the coat patterns of mammals (artiodactyls and carnivores) and ecological and behavioral variables.

	Ecological and behavioral variables associated with coat pattern	
Group	**Spots**	**Stripes**
Artiodactyla	Solitary‡[a], hiders‡[a], dense forest habitat*[a]	Solitary*[a], hiders*[a], dense forest*[a] and light forest‡[b] habitat
Cervids	Diurnal‡[b], not solitary*[b], hiders*[a], grassland/bushland habitat*[a]	NS
Bovids	Solitary*[a, b], hiders*[a], light forest habitat‡[a, b]	Hiders*[a], light forest habitat‡[a, b]
Carnivora	Arboreal‡, ungulate prey‡, closed environment‡	Arboreal*, terrestrial‡, grassland habitat‡
Canids	NA	NA
Ursids	NA	NA
Procyonids	NA	NA
Mustelids	NA	NA
Viverrids	Arboreal‡	NA
Herpestids	NA	NA
Hyaenids	NA	NS
Felids	Arboreal‡, forest habitat‡	NS

Asterisk (*), significant results of nonparametric chi-square or Fisher exact probability tests; ‡, significant results of phylogenetically controlled comparisons using MacClade and Maddison's concentrated changes tests (Maddison 1990).

NA, not applicable (no species showing that type of coloration); NS, not significant (no significant association found between coat pattern and ecological or behavioral variables).

a, young; b, adults.
Source: Ortolani and Caro 1996, Ortolani 1999, Stoner et al. 2003a.

photographs of gray squirrels show that countershading removes brightness gradients, although not completely, and only when specimens are placed horizontally (Kiltie 1989a). Across species, countershaded bovids and artiodactyls are diurnal and live in desert environments, as might be predicted under this hypothesis (Stoner et al. 2003a); similarly, countershaded lagomorphs are diurnal and live in grassland habitats (Stoner et al. 2003b), although most of these latter associations collapse after controlling for shared ancestry. Unfortunately, countershading itself cannot be taken as evidence that selection has acted to reduce shadow. A dark dorsum may be a device to reduce ultraviolet radiation or to counteract dorsal abrasion (Kiltie 1988). Also, if pigmentation is costly, background matching is a sufficient explanation for countershading, as animals would be expected to refrain from producing melanin below. Consider naked mole rats, which have dark dorsa but pink ventral surfaces and very short legs; they are fossorial but occasionally disperse above ground at night. Under these circumstances, dark backs are more likely to match the background when viewed by aerial predators rather than to help in minimizing shadow, in thermoregulation, or in protecting against ultraviolet light (Braude et al. 2001).

Communication

Patches of color, rather than overall coloration, may also be used to communicate to conspecifics. Intraspecific signals may help animals maintain visual contact, as between mothers and young (Leyhausen 1979); may function as social releasers (Fox 1971), that is, as signals of subordination or devices to intimidate rivals (Ewer 1973); may warn conspecifics that predators are close (Alvarez et al. 1976); or may signal reproductive condition, dominance, health, or even genetic quality to potential mates (Pagel 1994). Interspecific signaling may include *aposematism,* in which prey advertise their noxiousness or pugnacity; lures that deflect predatory attack away from the body; or lures that prevent prey from recognizing that a predator is present.

Intraspecific communication. The second major evolutionary force thought to be responsible for coloration of particular body parts is communication between conspecifics, but, unfortunately, the meaning of many of these signals is still opaque. Systematic evidence from artiodactyls, carnivores, and lagomorphs ties markings on the face, ears, legs, tail, and rump to intraspecific signaling, because these markings are associated with conditions in which they are most visible (diurnal activity and open habitats) and are seen in gregarious species (table 3). Specifically, white or dark faces are seen in social ungulates, as are white patches on the ears in forest-living carnivores, dark ear patches in group-living lagomorphs, and conspicuous legs in diurnal desert and grassland ungulates (figure 1e). Conspicuous tail coloration in ungulates is strongly associated with being diurnal and living in groups, whereas carnivores exhibit black tail tips in grassland habitats. Finally, ungulates with white rumps inhabit open

---

Box 2. Melanism in mammals.

While most mammals show gradual variation in color across populations, some populations exhibit discontinuous variation and are either white or black. Albinism is caused by a single genetic mutation that is thought to have no adaptive significance, since albinos are removed from populations rapidly. Melanism (black or very dark brown pelage), however, may be found in 20% of individuals in some populations. Most famously, it is seen in certain individual predators living in tropical forests, such as black panthers (melanistic jaguars), but it also appears in burnt areas and urban landscapes. For instance, fox squirrels that inhabit fire-climax pine savannas in the southeastern United States have light, dark, and intermediately colored morphs. There, the percentage of black hair on the dorsum is positively correlated with frequency of lightning-caused wildfires, as well as climatic factors that influence fires (Kiltie 1989b). Intermediate and black-backed morphs matched their background better than light morphs—only briefly, however, for just the first two weeks after an area had burnt (Kiltie 1992)—calling antipredator benefits into question. Nonetheless, red-tailed hawks responded more slowly to intermediate-colored morphs than to dark or light morphs, which could be sufficient to maintain melanistic alleles in the population (Kiltie and Laine 1992). Given that melanism could also be important for temperature regulation in humid habitats, such as tropical forests, the functional advantages (if any) are unclear.

---

habitats and are gregarious. Interpretation is tricky, however. For example, the association between white spots on the backs of the ears and living in forests, or between black ears and living in grasslands (both of which are found in felids), might either serve to let young follow their mothers (Ewer 1973) or be used in intraspecific fights when the ears are twisted forward to face an opponent (Hingston 1933).

Coloration as communication has been advanced most thoroughly in primates. Primates are particularly colorful not only because they sport different pelage hues but because some exhibit brightly colored patches of blue and red skin. Interspecific and intraspecific variation in fur color in primates is well described but poorly understood, because primate coloring is quite labile even among closely related species (see below). Additionally, in a number of primates, infants have coats that range from flamboyant to deep black or white, whereas parental coats are often agouti. Attempts to generate and test predictions concerning the function of primate natal coats have met with great difficulty. Straightforward matching of species to behavioral and ecological variables lends weight to ideas of avoiding infanticide (Treves 1997),
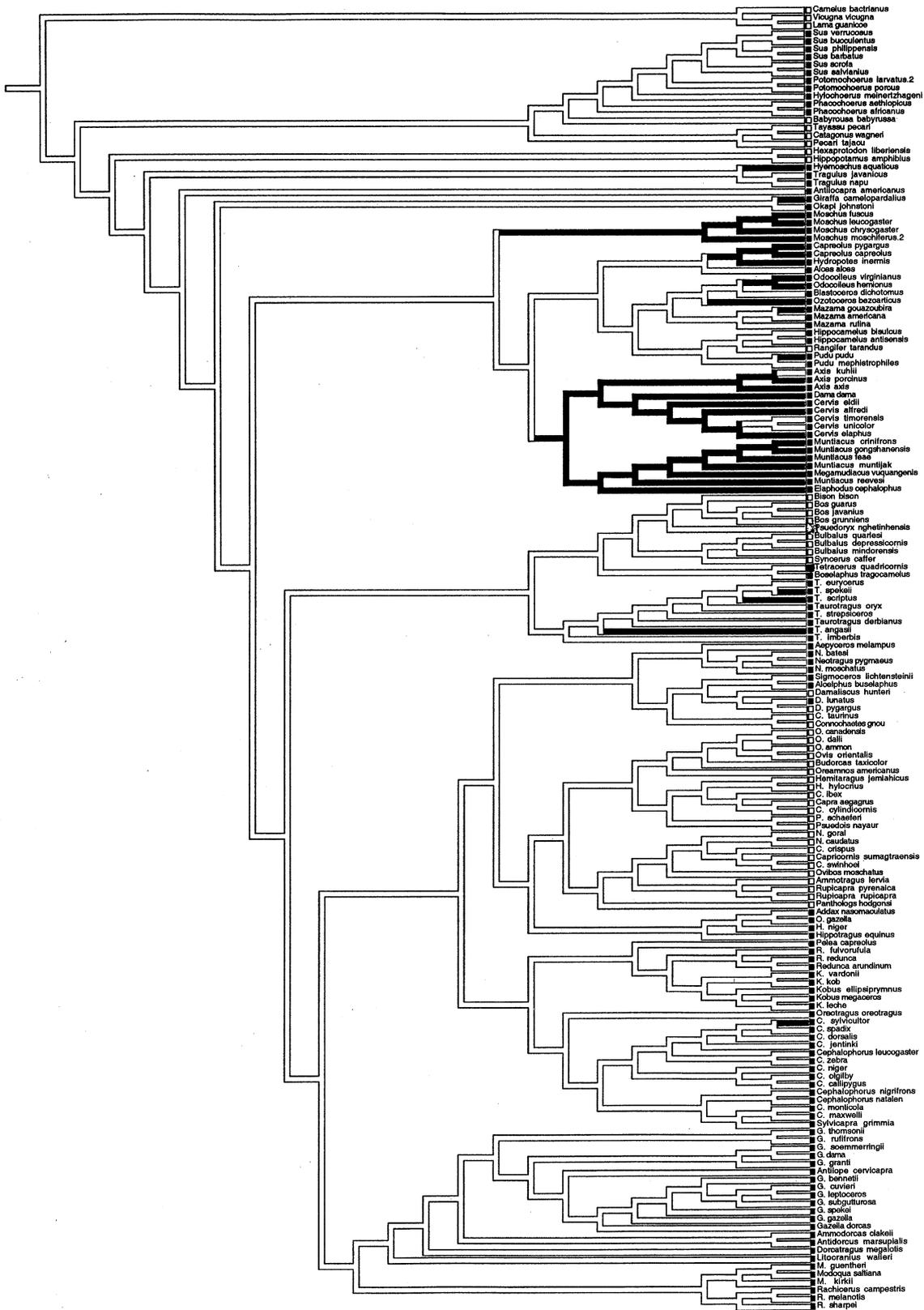
Figure 2. Association between spotted coats in young artiodactyls and hider species (species that sequester their young during the first weeks after birth). Black lines denote species with spotted coats, and white lines denote nonspotted species. Black boxes on the right denote species that are hiders; white boxes denote species that are not hiders. Source: Stoner and colleagues (2003a); © 2003 Oxford University Press, used with permission.

but tests employing phylogenetic controls fail to support these suppositions or other ideas about attracting the attentions of allomothers (individuals raising offspring that are not their own) (Ross and Regan 2000). Ideas that conspicuous coats might signal an animal's condition, or, conversely, that they are inconspicuous in natural settings, have yet to be explored, and at present the adaptive significance of natal coats in primates is an open question.

Sexual selection. In contrast to almost all other mammalian orders, primates display considerable sexual dichromatism (differences in the coloring of males and females), but the function of colorful patches on males (often associated with facial structures) or on females (usually sexual swellings) is poorly understood. In some species with polygynous or polygynandrous mating systems, males show colorful sexual skin that may be used in settling dominance relations, although there is debate over the means by which this occurs. Certainly, sexual skin plays some role in male–male displays. For example, the degree of scrotal "blueness" of male vervet monkeys (figure 1f) predicts dominance when unfamiliar males are paired (Gerald 2001). In species in which male sexual skin resembles that of females (e.g., hamadryas baboons), males may present to other males in order to mollify aggression (sociosexual mimicry; Wickler 1968), although much criticism has been leveled at this argument.

The adaptive significance of sexual skin coloration in female primates is perhaps marginally more straightforward. Sexual swellings around the buttocks and vulva are usually bright red and are found in 10% of primate species, having evolved three times in old-world monkeys and apes. Numerous hypotheses have been advanced for the function of these swellings, including advertising receptivity and, as a consequence, fostering male–male competition and confusing paternity (Nunn 1999). One recent analysis suggests that the size (length) of the swelling, at least in yellow baboons, is correlated with earlier age of reproduction, larger number of offspring born and surviving per annum, and higher proportion of offspring that survive; in other words, with female quality (Domb and Pagel 2001). Males compete over these high-quality females, grooming them more and suffering more aggression when they consort with them. While color per se was not measured in this study, bright color draws attention to the swollen area and therefore has all the features of an advertisement of female quality.

In contrast to birds (box 3), few other mammals show sexual dichromatism (although they do show considerable sexual dimorphism). Some male ungulates, such as eland, turn dark blue as adults or harem holders, but little more is known about this phenomenon. In lions, in contrast to other felids, females live in prides and males live in small coalitions. Unique among felids, male lions carry manes, some of which are black whereas others are sandy-colored like the rest of the coat. Black mane coloration is associated with higher food intake, with age, with testosterone concentrations, and with cooler environments. Dark-maned males are more likely to

---

Box 3. A brief history of research on coloration in birds.

Early discussions of bird coloration, including those between Darwin and Wallace (Blaisdell 1992), centered on species recognition, mate choice, and crypsis, but attention later turned to bright coloration in monomorphic species that was controversially viewed as advertising unprofitability or unpalatability (Baker and Parker 1979). Recent research has concentrated on explaining skin and feather coloration in the context of communication. Plumage badges, for example, are known to settle contests over food and breeding territories (Pryke and Andersson 2003), but most attention has focused on explaining sexual dichromatism, specifically, bright colors seen in males. In the last 15 years, a raft of studies have shown that females choose to mate with colorful males or with males sporting bright epaulets, head patches, or chest patches of feathers (Gustafsson et al. 1995). These variously correlate with male nest attentiveness, over-winter survival, or reproductive success, depending on the study; as a result of female preference, they consequently result in earlier laying dates and sometimes polygyny. In some species, the size of feather patches or the brightness and color of wattles and combs are associated with an absence of parasite load or with some other aspect of male condition. In particular, red or yellow feathers predict nutritional status, because they are carotenoid-based pigments that cannot be synthesized, only ingested (Hill et al. 2002), but even orange plumage produced by melanin pigments and blue-ultraviolet coloration produced by feather microstructure reflect male quality (Siefferman and Hill 2003). In short, colorful patches of feathers appear to be honest signals of male condition and are passed from fathers to sons. At this point it is not clear whether the extraordinary diversity of bird coloration patterns will eventually be interpreted principally in term of sexual selection, or whether this is a consequence of a sexual selection–driven research bias currently in vogue.

---

lead an approach toward playbacks of recorded male roars, and are more likely to survive wounding in fights that occur over access to prides. As a result, dark-maned males have longer reproductive life spans and higher offspring survival, possibly as a result of enhanced paternal protection against foreign infanticidal males. Unsurprisingly, lionesses prefer to mate with the darkest-maned male in their coalition. While dark manes indicate health and vigor, they are held in check by the disadvantages of overheating (West and Packer 2002).

Interspecific communication. The most famous example of aposematism in the animal kingdom is the spotted skunk,

Table 3. Summary of significance tests showing relationships between the occurrence of contrasting patches on the coats of mammals (artiodactyls, carnivores, and lagomorphs) and ecological and behavioral variables.

Group	Variables associated with contrasting patches on different parts of the body						
	Face (patch color/ appearance)	Throat (patch color/ appearance)	Ears (patch color/ appearance)	Legs (patch color/ appearance)	Tail (patch color/ appearance)	Side (patch color/ appearance)	Rump (white)
Artiodactyla	Intermediate group size (dark‡, white‡), large group size (dark‡), diurnal (white‡), grassland habitat (conspicuous‡)	NT	NT	Large group size (dark‡), diurnal (white‡), desert habitat (dark‡, conspicuous‡), grassland habitat (conspicuous‡)	Intermediate group size (dark*, conspicuous‡), large group size (dark*, white‡, conspicuous‡), diurnal (dark*, conspicuous‡)	Intermediate* or large‡ group size	Intermediate* or large* group size, diurnal‡, open environment‡
Cervids	Diurnal (dark*), grassland habitat (conspicuous‡)	NT	NT	NS	NS	NS	Intermediate‡ or large* group size
Bovids	Intermediate group size (dark‡), large group size (dark‡, conspicuous*)	NT	NT	NS	Large group size (dark*, conspicuous*), diurnal (dark*, white*, conspicuous‡)	NS	Intermediate* or large* group size, open environment‡
Carnivora	NT	NS	Forest (white‡)	NT	Nocturnal (ringed tail‡), diurnal (black tail tip*), arboreal (ringed tail‡), terrestrial (black tail tip‡), closed environment (ringed tail‡), grassland habitat (black tail tip‡, white tail tip‡), forest habitat (ringed tail‡)	NS	NS
Canids	NT	NS	NS	NT	NS	NT	NT
Ursids	NT	NA	NS	NT	NA	NT	NT
Procyonids	NT	NA	Groups (conspicuous‡)	NT	NA	NT	NT
Mustelids	NT	NS	Forest habitat (white‡)	NT	Grassland (black tail tip*)	NT	NT
Viverrids	NT	Groups (white‡)	NS	NT	NS	NT	NT
Herpestids	NT	NS	NS	NT	Grassland (black tail tip*)	NT	NT
Hyaenids	NT	NA	NS	NT	NS	NT	NT
Felids	NT	NS	Forest habitat (white‡), grassland habitat (black‡)	NT	NS	NT	NT
Lagomorpha	NT	NT	Groups (dark‡), not diurnal (dark*), not closed environment (white*)	NT	Groups (white‡), burrows (white‡), no burrows (dark*), grassland habitat (white‡)	NT	NT

Asterisk (*), significant results of nonparametric chi-square or Fisher exact probability tests; ‡, significant results of phylogenetically controlled comparisons using MacClade and Maddison's concentrated changes tests (Maddison 1990).

NA, not applicable (no species showing that type of coloration); NS, not significant (no significant association found between contrasting coat patches and ecological or behavioral variables); NT, not tested.

Source: Ortolani and Caro 1996, Ortolani 1999, Stoner et al. 2003a, 2003b.

which has contrasting black and white patches of fur on its body. Seven species of mustelid have black-and-white coats, and all produce noxious anal secretions, a highly significant association after controlling for phylogeny (figure 3). Similarly, light tails are associated with the production of these secretions in mustelids and herpestids, as are black undersides in the latter family. Black-and-white coloration may even warn of pugnacity, as suggested for the ratel (Estes 1991), and may advertise quills and spines, as seen in some species of porcupines and tenrecs.

More subtly, artiodactyls and lagomorphs use color patches to enhance pursuit-deterrent signals aimed at predators. These signals may inform an approaching predator that it has been detected (perception advertisement); they may also inform the predator of the prey's condition and hence its probability of escaping (quality advertisement; Caro 1995). For instance, when pursued by wild dogs, Thomson's gazelles stot vigorously (a stylized gait with legs held stiff and straight) and lift their tails, perhaps to flaunt their white rump patch (FitzGibbon and Fanshawe 1988). Pursuit-deterrent signals might therefore be expected to be directed at stalking predators, and it is interesting that both dark and white tails are seen in artiodactyls that are principally attacked by stalkers. By contrast, quality advertisement might be directed at coursing predators, and both white rumps and dark faces are associated with pursuit by coursers in bovids and artiodactyls (Stoner et al. 2003a). The size or brightness of color patches could be related to condition in ungulates, although this has never been tested.

Finally, patches of color may be used to attract heterospecifics' attention to particular areas of the body. Ortolani (1999) found that carnivores with white tail tips were species that preyed on bovids or small mammals, raising the intriguing possibility that rapid flicking of the tail tip may distract or lure prey, as occurs in some snakes. She noted also that white tail tips in carnivores (but not black tips) were associated with predation by raptors. In a singular experiment that has never been followed up, Powell (1982) trained three red-tailed hawks to attack various weasel models that were towed across an experimental arena. The hawks consistently missed attacking models with a black tail tip but struck those with a black mark on the body, suggesting that black tips may distract avian predators or draw them to a less vulnerable area of the body.

Physiological hypotheses

The final major class of hypotheses for coloration in mammals concerns a potpourri of physiological and physical functions that are involved in regulating body temperature (by reflecting or absorbing radiation, or by providing a surface that
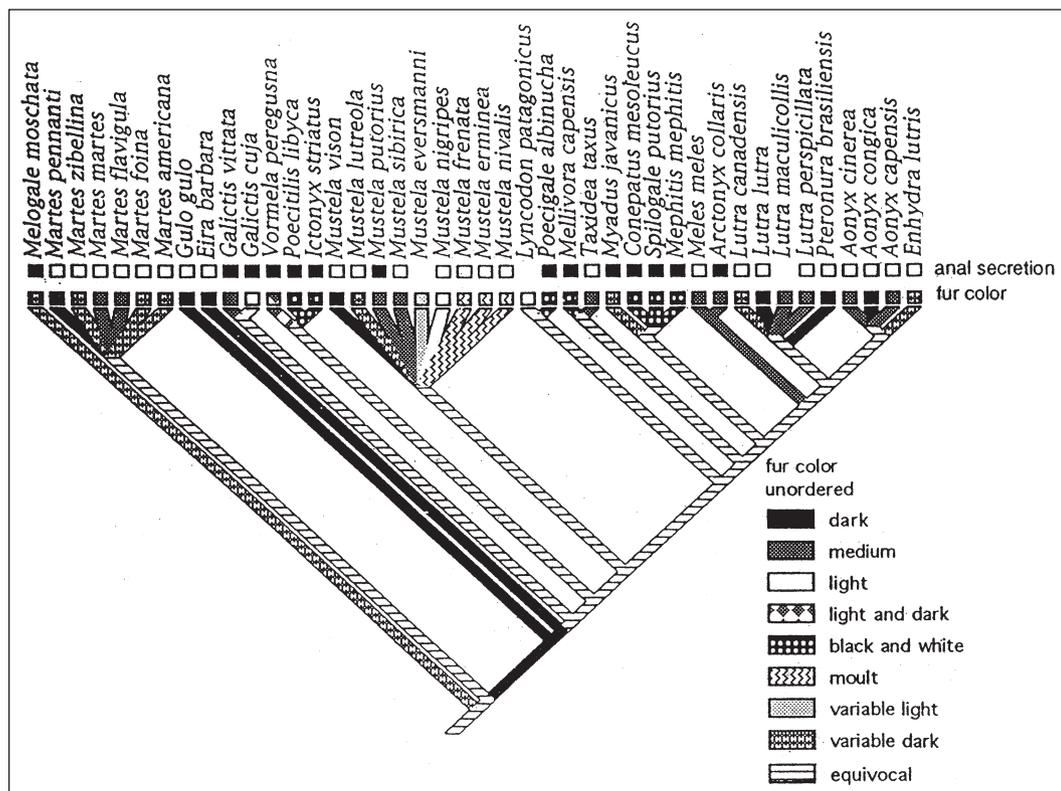
Figure 3. Phylogeny of the Mustelidae, showing the reconstructed evolution of fur color; equivocal branches denote ambiguities in character reconstruction. The row of boxes labeled "anal secretion" denotes whether the species possess a noxious anal sac secretion (black box) or not (white box); data for three species are missing for this character. Source: Ortolani and Caro (1996); © 1996 Cornell University Press, used with permission.

Table 4. Summary of significance tests showing the relationships between the coloration of mammals (artiodactyls, carnivores, and lagomorphs) and ecological and behavioral variables.

| | Variables associated with mammal coloration | | | | |
Group	Uniform coloration (color)	Face markings (color)	White rump	Dark eye markings (type of mark)	Dark tail
Artiodactyla	Closed environment (dark*), tropics (dark†), dense forest (dark*)	Grassland (white†)	Desert*, grassland*	NT	NT
Cervids	Dense forest (dark*)	Open environment (white†)	Desert*	NT	NT
Bovids	Closed environment (dark*), tropics (dark†), dense forest (dark*), swamp (dark*)	Desert (white*), grassland (white*)	Desert*, grassland*	NT	NT
Carnivora	Tropical forest (dark†)	NT	NT	Open and closed environment (eye patch†), small body size (eye patch†), terrestrial (eye contour†), crepuscular (eye contour†, eye patch†), riparian (marking below eye†, eye patch†), grassland (eye contour†)	NS
Canids	Tropical forest (dark†)	NT	NT	Crepuscular (marking below eye†)	NT
Ursids	Tropical forest (dark†)	NT	NT	NS	NT
Procyonids	NS	NT	NT	NS	NT
Mustelids	NS	NT	NT	Diurnal (marking below eye†)	NT
Viverrids	NS	NT	NT	NS	NT
Herpestids	Tropical forest (dark†)	NT	NT	NS	NT
Hyaenids	NS	NT	NT	NS	NT
Felids	NS	NT	NT	NS	NT
Lagomorpha	Tropics (dark*)	NT	NT	NS	Arctic*, high latitude*

Asterisk (*), significant results of nonparametric chi-square or Fisher exact probability tests; †, significant results of phylogenetically controlled comparisons using MacClade and Maddison's concentrated changes tests (Maddison 1990).

NS, not significant (no significant association found between coloration and ecological or behavioral variables); NT, not tested.

Source: Ortolani and Caro 1996, Ortolani 1999, Stoner et al. 2003a, 2003b.

enhances or reduces evaporation) and reducing glare from the sun, although predictions regarding these functions vary according to whether skin or hair color is under discussion, and depend on physical properties of hair follicles (box 4; Walsberg 1983). While there is reasonably strong correlational evidence to bolster the idea of an adaptive physiological function for mammal coloration, its precise mechanisms remain hazy. The chief finding from phylogenetically controlled comparisons is that artiodactyls, carnivores, and perhaps lagomorphs obey Gloger's rule, in that dark overall pelage is associated with species that live in the tropics (table 4). Unfortunately, we do not know why dark fur is advantageous in tropical areas, particularly in forests, a humid habitat. Is it to keep the animal dry through enhanced evaporation from warm surfaces, or to aid in concealment? A second finding suggests that white face markings in ungulates, and possibly white rump patches, are instrumental in reducing heat load in open desert or grassland habitats because they reflect heat. Both parts of the body can be turned toward or away from the sun to regulate reflectance. Third, dark eyes are found in crepuscular and riparian species, suggesting that they counteract glare when the sun is horizontal or reflected off water (Ortolani 1999); indeed, Eskimos rub soot around their eyes to prevent snow blindness. Last, dark tails are found in lagomorphs living in cold climes, which may indicate differential melanocyte production in colder areas of the body. While robust, these findings have few conceptual underpinnings in common, except that they are all linked by being unrelated to concealment or communication.

Nonadaptive explanations

It would normally be improper to consider anything other than adaptive explanations for most biological traits, but there are hints of nonadaptive patterns of coloration in mam-

Box 4. The physiological basis of external coloration.

Agouti, a banded pattern appearing grey or brown, is probably the ancestral pelage color of mammals. Fur color derives primarily from melanin-based pigmentation deposited in shafts of hair, and thus differs from the hemoglobin that provides the red hue of primate sexual swellings and occasionally facial skin patches. Agouti is produced by alternating black eumelanin and reddish phaeomelanin banding on hairs. As reddish bands are reduced in number, pelage transforms from agouti to dark brown (black with little red). If depigmentation continues, black is lost, leading to light gray, silvery, cream-colored, and eventually colorless hair. If black bands are lost, however, pelage transforms from agouti to reddish-brown (red with little black). Then, if depigmentation continues, pelage turns red, orange, gold, straw, cream, and eventually colorless (Hershkovitz 1977).

Variation in pelage coloration is found in most populations. During development, both genetic and environmental influences, including ambient temperature, affect coat color. Coat color does not necessarily remain static throughout an animal's life; depigmentation may occur as a result of acute stress or age. Furthermore, in a minority of species, young have characteristic natal coats that differ from adult pelage. These include spotted coats in many artiodactyls (e.g., peccaries) and some felids (e.g., pumas), and black, cream, or ostentatious natal coats in some primates (e.g., gibbons).

Skin color is dependent on the melanic layer in the dermis. A blue hue is caused by light impinging on the melanic layer in the dermis and being reflected back through the epidermis; the way that the light scatters, and hence its hue, depends on the collagen and water content of the skin. Red skin results from a plexus of thin-walled blood vessels just below the epidermis. The degree of redness is linked to testosterone production in males and to increases in circulation during follicular development in females (Dixson 1998). Skin color is therefore more labile than fur color and is a priori more likely to signify short-term changes in health.

mals. In particular, forest-living guenons have an extraordinary diversity of facial and body coloration patterns (Kingdon 1988), and tamarins and marmosets show radically different hues on their foreheads, crowns, napes, mantles, and tails, even within species (Hershkovitz 1968). Along the headquarters of just one river, the Rio Jurua in Brazilian Amazonia, saddleback tamarins of both sexes show at least five color morphs ranging from blackish-brown to white, but chromatic types are radically different on opposite sides of the river, a known barrier to genetic dispersal as determined from mitochrondrial cytochrome *b* sequencing. Given that ecological factors and predation pressures are likely to be virtually identical on both river banks, it is difficult not to infer genetic drift as an explanation for different color morphs (Peres et al. 1996). More generally, there is a possibility that certain (unknown) selection pressures, which would constrain coloration over many parts of the body, are lifted for monkeys living in tropical rainforests (Hershkovitz 1968).

More children's questions

Classic hypotheses for selective advantages of coloration were among the first offered to vindicate Darwin's theory of natural selection (Blaisdell 1992), but only now are they receiving the systematic attention that they deserve. That said, many explanations are still *post hoc* and urgently require experimental testing. At present, most biologists believe that crypsis is the key evolutionary force driving the agouti-colored pelage observed in so many mammals. Nonetheless, it is still not clear why some species turn from agouti to white in winter while other sympatric species do not, nor can we yet explain the quite different striking coloration in species such as the giant panda or Burchell's zebra. Intraspecific communication is obviously important in explaining patches of color on the faces, ears, legs, and tails of mammals, but we are a long way from pinning down the content of these signals or understanding what observers they target (e.g., predators, prey, or potential mates). The virtual absence of sexual dichromatism in mammals, in spite of the prevalence of polygyny, remains a mystery; it stands in sharp contrast to the often striking differences between male and female coloration in birds, whose coloration is so important in intra- and intersexual displays. Superficially, this suggests a far smaller role of female choice in mammals than in birds. Aposematism, a clear example of interspecific signaling, explains coloration in mustelids, but why should mustelids need to be so noxious or pugnacious when other sympatric carnivores are not? Finally, although physical factors appear responsible for some types of coloration, we don't know why they are important in some environments but not in others; and 170 years after Gloger formulated his rule, we still don't understand why mammals obey it. Those "why" questions that children are so fond of have no easy answers. Better to ask them a trick question back: Which mammal is green?

Acknowledgments

References cited
Alvarez F, Braza F, Norzagaray A. 1976. The use of the rump patch in the fallow deer (*D. dama*). Behaviour 56: 298–308.
Baker RR, Parker GA. 1979. The evolution of bird colouration. Proceedings of the Royal Society of London, B 287: 63–130.

Belk MC, Smith MH. 1996. Pelage coloration in oldfield mice (*Peromyscus polionotus*): Antipredator adaptation? Journal of Mammalogy 77: 882–890.

Blaisdell ML. 1992. Darwinism and Its Data: The Adaptive Coloration of Animals. New York: Garland.

Braude S, Ciszek D, Berg NE, Shefferly N. 2001. Ontogeny and distribution of countershading in colonies of the naked mole-rat (*Heterocephalus glaber*). Journal of Zoology 253: 351–357.

Burtt EH Jr. 1981. The adaptiveness of colors. BioScience 31: 723–729.

Caro TM. 1995. Pursuit-deterrence revisited. Trends in Ecology and Evolution 10: 500–503.

Cott HB. 1940. Adaptive Colouration in Animals. London: Methuen.

Dixson AF. 1998. Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings. Oxford (United Kingdom): Oxford University Press.

Domb LG, Pagel M. 2001. Sexual swellings advertise female quality in wild baboons. Nature 410: 204–206.

Endler JA. 1978. A predator's view of animal colour patterns. Evolutionary Biology 11: 319–364.

———. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315–352.

Estes RD. 1991. The Behavior Guide to African Mammals. Berkeley: University of California Press.

Ewer RF. 1973. The Carnivores. Ithaca (NY): Cornell University Press.

FitzGibbon CD, Fanshawe J. 1988. Stotting in Thomson's gazelles: An honest signal of condition. Behavioral Ecology and Sociobiology 23: 69–74.

Fox MW. 1971. Behavior of Wolves, Dogs and Related Canids. New York: Harper and Row.

Gerald MS. 2001. Primate color predicts social status and aggressive outcome. Animal Behaviour 61: 559–566.

Gloger CWL. 1833. Das Abändern der Vögel durch Einfluss des Klimas. Breslau (Germany): A. Schulz.

Gustafsson L, Quarnström A, Sheldon BC. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature 375: 311–313.

Hershkovitz P. 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colors. Evolution 22: 556–575.

———. 1977. Living New World Monkeys (Platyrrhini). Chicago: Chicago University Press.

Hill GE. 2002. A Red Bird in a Brown Bag: The Function and Evolution of Colorful Plumage in the House Finch. New York: Oxford University Press.

Hill GE, Inouye CY, Montgomerie R. 2002. Dietary carotenoids predict plumage coloration in wild house finches. Proceedings: Biological Sciences 269: 1119–1124.

Hingston RWG. 1933. The Meaning of Animal Colour and Adornment. London: Edward Arnold.

Kaufman DW. 1974. Adaptive coloration in *Peromyscus polionotus:* Experimental selection by owls. Journal of Mammalogy 55: 271–283.

Kiltie RA. 1988. Countershading: Universally deceptive or deceptively universal? Trends in Ecology and Evolution 3: 21–23.

———. 1989a. Testing Thayer's countershading hypothesis: An image processing approach. Animal Behaviour 38: 542–544.

———. 1989b. Wildfire and the evolution of dorsal melanism in fox squirrels *Sciurus niger*. Journal of Mammalogy 70: 726–739.

———. 1992. Tests of hypotheses on predation as a factor maintaining polymorphic melanism in coastal-plain fox squirrels (*Sciurus niger* L.). Biological Journal of the Linnean Society 45: 17–37.

Kiltie RA, Laine AF. 1992. Visual textures, machine vision and animal camouflage. Trends in Ecology and Evolution 7: 163–166.

Kingdon J. 1988. What are face patterns and do they contribute to reproductive isolation in guenons? Pages 227–245 in Gautier-Hion A, et al., eds. A Primate Radiation: Evolutionary Biology of the African Guenons. New York: Cambridge University Press.

Leyhausen P. 1979. Cat Behaviour: The Predatory and Social Behaviour of Domestic and Wild Cats. New York: Garland STPM Press.

Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: Are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44: 539–557.

Merilaita S. 1998. Crypsis through disruptive coloration in an isopod. Proceedings: Biological Sciences 265: 1059–1064.

Nunn CL. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signals hypothesis. Animal Behaviour 58: 229–246.

Ortolani A. 1999. Spots, stripes, tail tips and dark eyes: Predicting the function of carnivore colour patterns in carnivores using the comparative method. Biological Journal of the Linnean Society 67: 433–476.

Ortolani A, Caro TM. 1996. The adaptive significance of color patterns in carnivores: Phylogenetic tests of classic hypotheses. Pages 132–188 in Gittleman J, ed. Carnivore Behavior, Ecology, and Evolution. Ithaca (NY): Comstock Press.

Pagel M. 1994. The evolution of conspicuous oestrous advertisement in Old World monkeys. Animal Behaviour 47: 1333–1341.

Peres CA, et al. 1996. Riverine barriers and gene flow in Amazonian saddleback tamarins. Folia Primatologica 67: 113–124.

Poulton EB. 1890. The Colours of Animals. New York: Appleton.

Powell RA. 1982. Evolution of black-tipped tails in weasels: Predator confusion. American Naturalist 119: 126–131.

Pryke SR, Andersson S. 2003. Carotenoid epaulettes reveal male competitive ability: Experiments with resident and floater red-shouldered widowbirds. Animal Behaviour 66: 217–224.

Ross C, Regan G. 2000. Allocare, predation risk, social structure and natal coat colour in anthropoid primates. Folia Primatologica 71: 67–76.

Siefferman L, Hill GE. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. Behavioral Ecology 14: 855–861.

Stoner CJ, Caro TM, Graham CM. 2003a. Ecological and behavioral correlates of coloration in artiodactyls: Systematic analyses of conventional hypotheses. Behavioral Ecology 14: 823–840.

Stoner CJ, Bininda-Emonds ORP, Caro T. 2003b. The adaptive significance of colouration in lagomorphs. Biological Journal of the Linnean Society 79: 309–328.

Sumner P, Mollon JD. 2003. Colors of primate pelage and skin: Objective assessment of conspicuousness. American Journal of Primatology 59: 67–91.

Thayer AG. 1909. Concealing Coloration in the Animal Kingdom. New York: Macmillan.

Treves A. 1997. Primate natal coats: A preliminary analysis of distribution and function. American Journal of Physical Anthropology 104: 47–70.

Wallace AR. 1889. Darwinism. New York: Humboldt.

Walsberg GE. 1983. Coat color and solar heat gain in animals. BioScience 33: 88–91.

West PM, Packer C. 2002. Sexual selection, temperature, and the lion's mane. Science 297: 1339–1343.

Wickler W. 1968. Mimicry in Plants and Animals. New York: McGraw-Hill.