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Contrasting coloration in terrestrial mammals

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Here I survey, collate and synthesize contrasting coloration in 5000 species of terrestrial mammals focusing on black and white pelage. After briefly reviewing alternative functional hypotheses for coloration in mammals, I examine nine colour patterns and combinations on different areas of the body and for each mammalian taxon to try to identify the most likely evolutionary drivers of contrasting coloration. Aposematism and perhaps conspecific signalling are the most consistent explanations for black and white pelage in mammals; background matching may explain white pelage. Evidence for contrasting coloration is being involved in crypsis through pattern blending, disruptive coloration or serving other functions, such as signalling dominance, lures, reducing eye glare or in temperature regulation has barely moved beyond anecdotal stages of investigation. Sexual dichromatism is limited in this taxon and its basis is unclear. Astonishingly, the functional significance of pelage coloration in most large charismatic black and white mammals that were new to science 150 years ago still remains a mystery.

Keywords: aposematism; black and white pelage; communication; crypsis; sexual dichromatism

1. INTRODUCTION

Since zoologists first tried to explain the function of coloration in animals, they have debated the significance of black and white coats in mammals. For example, Wallace and Darwin sparred over whether the stripes of zebra *Equus burchelli* were conspicuous or not (Wallace 1891); and Poulton (1890), Beddard (1892) and Hingston (1933) argued that zebra stripes resembled the background whereas Thayer (1909) and Cott (1940) thought they were disruptive. They also discussed coloration of Malayan tapirs *Tapirus indicus*, giant anteaters *Myrmecophaga tridactyla*, skunks (Mephitidae) and giant pandas *Ailuropoda melanoleuca*.

Patches of black fur and white fur juxtaposed against each other are arguably a special form of coloration because they generate such striking contrast compared with other colour combinations. Conspicuous coloration immediately evokes aposematism or communication (Wallace 1889) but this cannot be assumed because (i) disruptive coloration is also characterized by contrasting colours (Cott 1940), (ii) colour patterns can be both aposematic and cryptic depending on the distance from which they are viewed (Gomez & Thery 2007) and (iii) pattern blending may be involved in those species living in dark shadow, or white snow and ice (Thayer 1909).

Unfortunately, there has been systematic attempt neither to test different theories of coloration with respect to black and white pelage in mammals nor even to document its distribution comprehensively. Therefore, after briefly reviewing theories of coloration, I set up mutually exclusive predictions for each theory using design features and socio-ecological correlates of colour patterns in terrestrial mammals (table 1). Then I categorize species into 11 different groupings based principally on the placement and pattern of black and white patches of fur on the body. Last, I use the predictions to reach potential conclusions for species-specific functions of contrasting coloration in mammals. This survey is comprehensive although not exhaustive and it is necessarily imprecise: intraspecific differences in coloration are poorly documented for most species, particularly the extent to which coloration varies seasonally or across individuals (Hershkovitz 1968); and the natural history of many of these species is scanty, especially their ambient light conditions and habitat coloration (Endler 1978). Furthermore, this assessment of coloration necessarily hinges on the assumption that non-humans view black and white coloration in approximately the same way as humans (Sumner & Mollon 2003; Stevens *et al.* 2007). Nonetheless, my goal is to set an agenda for asking appropriate functional questions about pelage coloration in this taxon.

2. THEORIES OF COLORATION

Animals that signal their unprofitability to potential predators are often bright red, orange, yellow or white in combination with black (Cott 1940). Such colours distinguish the bearer from green vegetation and from cryptic prey (Sherratt & Beatty 2003). Aposematic signals are often characterized by blocks of colour with sharp borders that are easy to discriminate, and sometimes by repeated colour patterns. In insects, aposematism is often associated with unpalatability, whereas in mammals it can be a marker of unprofitability that includes defences and perhaps even speed (table 1). In mammals, species with armoured

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Table 1. Some predictions about the design features, ecological and social correlates of black and white coloration patterns in terrestrial mammals. (X denotes supports hypothesis.)

		crypsis								
	apo[a]	BM	PB	DC	CS	sig	lure	SS	temp	AG
design features										
shape										
same as background		X	X							
same area as background		X	X							
large blocks	X							X		
regular patterns	X									
location										
patterns found at edge				X						
borders do not follow outline				X						
borders do follow outline					X					
light ventrum/dark dorsum					X					
proximal view						X[b]				
distal view						X[c,d]				
tail tip white or black						X[d]	X			
contrast										
high contrast	X			X						
ecological correlates										
lives in one habitat		X	X						X	
diurnal						X			X	
nocturnal/crepuscular		X								X
lives in snow		X							X	X
lives in shadow		X								
lives with no shade									X	X
social correlates										
solitary		X	X	X						
social species										
found in only one sex								X		
polygynous								X		
defences										
small body size		X								
medium body size	X									
spines	X									
toxic secretions	X									
speed	X									

[a] Apo, aposematism; BM, background matching; PB, pattern blending; DC, disruptive coloration; CS, countershading; sig, conspecific signal; SS, sexual selection; Temp, temperature regulation; AG, anti-glare.
[b] Badges of dominance.
[c] Pursuit deterrence signal or readiness to mate.
[d] Follow-me signals.

defences (including spines) are of middling body weight (Lovegrove 2001).

The other way to avoid predation is through crypsis that is achieved in three ways in mammals: (i) background matching, where large parts of the body resemble the general colour of the environment (Poulton 1890; Merilaita *et al.* 2001), and includes pattern blending, where spotted, striped or mottled coats resemble the shape and size of dappled patches of light and shade in the environment (Poulton 1890; Thayer 1909; Cott 1940). In both cases, the colour of individuals may be adapted to live in a circumscribed habitat (but see Houston *et al.* 2007). Since cryptic coloration is often found in mammals that hide or freeze upon seeing predators (Cott 1940; Caro 2005*a*), it might be expected in species that are behaviourally inconspicuous (i.e. are nocturnal, of small body size or solitary). (ii) Disruptive coloration, wherein blocks of highly contrasting coloration and sharp boundaries that sometimes lie perpendicular to the body outline are thought to prevent the predator from detecting or recognizing the prey's outline, or shape of its eye (Merilaita 1998; Schaefer & Stobbe 2006; Stevens *et al.* 2006). Again, solitary prey might benefit most. (iii) Countershading, where a light ventrum is thought to counteract shadow cast by the animal's upper surface on its lower surface (Kiltie 1988). Under countershading, a gradual change of contrast between dorsal and ventral fur is expected (Ruxton *et al.* 2004).

Colour patches may also be used as intraspecific signals and placement of these patches on the body often hints at their function. For example, badges of dominance are likely to be at the front of the animal whereas indicators of body condition that signal an ability to avoid predators or a readiness to mate are likely to be at the rear. Marks of recognition, facilitating individuals following one another, are likely to be on the rear-facing surface of pinnae, on rumps or tails

(Ortolani 1999). Patches of colour on the tail may also be used to mesmerize potential prey or to distract predators away from vulnerable parts of the body (Stevens 2005).

If coloration is sexually selected, colour patches may be expected only in one sex, particularly in polygynous species, where males compete intensely over females or where females choose mates (Hill 2006; Senar 2006). Some mammals have brightly coloured ornaments that may be involved in mate choice (electronic supplementary material).

Additionally, pelage coloration may influence thermoregulation with either dark and white hairs increasing or decreasing heat gain depending on hair structure, density, aspect and wind velocity (Walsberg 1983). Eumelanin in black skin or fur can protect against ultraviolet radiation (Diamond 2005) especially on dorsal surfaces. Management of radiation might be expected principally in diurnal species living in very hot or cold environments. Finally, if black patches around the eyes reduce reflected glare from fur or skin entering the eye, they can be expected to be in habitats with much reflectance and in crepuscular species that normally shun glare (Ficken *et al.* 1971).

3. BLACK AND WHITE MAMMALS

I restrict this survey to adults of approximately 5000 species of terrestrial mammals that have contrasting coloration focusing on those with both black (or dark) and white (or light) patches of fur, modified fur or skin on their body and/or appendages. I used Nowak (1999) and Macdonald (2006) extensively. I excluded albinos, melanistic and other polymorphisms, species with infants showing radically different pelage colour from adults (e.g. silver leaf monkey *Trachypithecus villosus*), and species of uniform appearance (e.g. Cape buffalo *Syncerus caffer*), except those with uniformly white pelage, and all pinnipeds and cetaceans because background lighting conditions for marine mammals are difficult to fathom. Principally, I considered species that had black and white patterns on the head, body, legs or tail. My restrictions are somewhat arbitrary, but I want to explain the juxtaposition of obviously contrasting pelage patches in a class of vertebrate generally thought to be drab and cryptic (Krupa & Geluso 2000; Caro 2005*b*; Lai *et al.* 2008). Viewed in this way, white and black coloration in mammals is a conundrum.

(a) *Black and white quills*

The short-nosed echidna *Tachyglossus aculeatus*, streaked tenrec *Hemicentetes semispinosus*, juvenile common tenrec *Tenrec ecaudatus*, hedgehogs (Erinaceidae), New World porcupines (Erethizontidae) and Old World porcupines (Hystricidae) have quills or spines on their dorsal and lateral surfaces. Spines are either white or yellow with black tips (echidnas and the North American porcupine *Erethizon dorsatum*), wholly black and white (tenrecs), white or yellow with black hairs below (New World porcupines), or with black or brown and white bands often with white or yellow tips (hedgehogs and Old World porcupines). Certain arboreal spinyrats (*Echimys*) have white median facial stripes and white tails. If disturbed, echidnas rapidly dig holes and erect spines to lodge themselves, or roll into a ball. Streaked tenrecs rub their quill tips together to make high-frequency sounds, vocalize and foot stamp. Hedgehogs jump backwards or butt their heads at predators, hissing, snorting and screaming, and roll into a ball. Porcupines emit odour, amble noisily, erect their spines, rattle quills, clack teeth and stamp their feet when disturbed (the crested rat *Lophiomys imhausi*, a possible porcupine mimic, shows the same rowdy behaviour); they can be pugnacious, backing into predators and, in some New World species, lashing out with their spiny prehensile tail. Some porcupine species have easily detachable spines, others that break at the tip; both kinds can lodge beneath an attacker's skin and can work into muscle.

These diverse auditory and olfactory advertisements in species that carry defensive spines force us to conclude that black/brown, and white/yellow coloration must also be aposematic, at least when viewed in close up, although predators' reactions to seeing spines is anecdotal or lacking (table 2). There is no explanation as to why other mammals with spines in the Tenrecidae, Cricetidae, Muridae, Platacanthomyidae, Echimyidae and Thyronomyidae do not show black and white coloration.

(b) *Horizontal bands of white fur on head, nape or dorsum, or on tail or in combination*

Members of the Mustelidae, Mephitidae and Herpestidae fall into this category and include the Patagonian weasel *Lyncodon patagonicus*, zorilla *Ictonyx striatus*, hog badger *Arctonyx collaris*, stink (*Mydaus*) and ferret badgers (*Melogale*), hog-nosed skunks (*Conepatus*) and Malagasy broad-striped mongoose *Galidictis fasciata*. This coloration stands out at night, a time when all these species are active. There is great unexplained variability in coloration within species; for example, in some striped skunks, *Mephitis mephitis*, there is only white along the forehead, in others only on the top and sides of the tail and in some others there are two bands of white on each side of the spine. Indeed, no two spotted skunks *Spilogale putorius* have the same pattern of broken white stripes along back and sides.

The function of white markings on a dark background in mephitids (skunks and stink badgers) is a textbook example of aposematism by which attackers are warned first by a sudden erection of a white tail, then a handstand and possibly bipedal advance, that a jet of foul smelling fluid could be accurately ejected at them from anal glands (Lariviere & Messier 1996). Spray causes extreme discomfort in domestic dogs and, by extension, natural predators (Hunter & Caro in press). Other signals include stamping, scratching and hissing.

Mustelids and herpestids have anal gland secretions that are less pungent than in mephitids (Macdonald 1985). Many mustelids are extremely pugnacious: wolverines *Gulo gulo* drive bears and cougars *Puma concolor* from kills; ratels *Mellivora capensis*, with their thick, almost impenetrable loose skin, attack animals far larger than themselves (Estes 1991); and both American *Taxidea taxus* and European badgers *Meles meles* have a ferocious reputation. Unlike morphological and physiological defences, hyper-aggressive behaviours are not recognized as consistent, reliable defences in these genera and consequently white dorsa are not generally acknowledged as a form of aposematism in mustelids. Mullerian mimicry of mephitids and background matching are additional possibilities: young wolverines born in the early Palaearctic spring are white, badgers appear grizzled and even spotted skunk coats appear dappled at a distance.

Striped possums (*Dactylopsila*) have three parallel black stripes on their head superimposed on a white or grey background and with a white tip to their tail. When angered, they give out a throaty gurgling shriek. All four species have an unpleasant and penetrating odour, potentially a case of convergent aposematism with mephitids.

Another family with dorsal or lateral white stripes is Myrmecophagidae (anteaters or tamanduas). Giant anteaters have a black wedge that extends from their chest and neck to top of the tail flanked by a thin white line above; southern tamanduas *Tamandua tetradactyla* have a white head, nape and rump. Both species have formidable foreclaws used to open termitaria and slash at attackers. Interestingly, giant anteaters have black and white bracelets of fur and southern tamanduas have white forearms that may draw attention to their weaponry (in a similar way that porcupine spines are aposematic, Speed & Ruxton 2005). Few observations of natural predators facing anteaters are recorded (but see Hingston 1933) leaving speculation about aposematism being based on similar fur coloration to mephitids and possession of dangerous claws (table 2).

Some subspecies of uakaris (*Cacajao*) have intriguing white dorsa. Piebald shrews *Diplomesodon pulchellum* have greyish upperparts with an elongated oval patch of white in the middle of the back and white underparts. Some shrews have poisonous saliva, and many smell foul, symptomatic of aposematism, but coloration may be a beacon for piebald shrew pups that scamper in a line, biting each others' rumps, with their mother at the helm.

(c) *Black and white face masks*

Many mid-sized carnivores in Canidae, Procyonidae, Mustelidae, Mephitidae and Viverridae families have black circles around the eyes but white on muzzles, cheeks or above the eyes. Others have black bands that run in an anterior–posterior direction through the eye separated by a white median facial stripe. As examples, the raccoon dog *Nyctereutes procyonoides* has a large dark spot beneath and behind the eye, the red panda *Ailurus fulgens* has black 'tears' on a white face, the black-footed ferret *Mustela nigripes* has a black 'bandit' mask over a white face and the masked palm civet *Paguma larvata* has a median white facial stripe and a white mark above and below each eye.

As many carnivores suffer from intraguild predation (Palomares & Caro 1999; Donaldio & Buskirk 2006), Newman *et al.* (2005) used natural history and semi-quantitative data to argue that, in species that are primarily terrestrial and living in open habitat with few available refuges, face masks are aposematic deterring larger carnivores. Many of these mid-sized species are foul smelling and aggressive (e.g. polecats *Mustela putorius*) and additionally have white markings on the nape, dorsum and tail. Focusing on the presence or absence of a dark eye contour around the eye or a patch below it, rather than contrasting face markings, Ortolani (1999) concluded, using phylogenetically controlled comparisons, that these patterns were instead anti-glare devices. Disruption of the face and hiding eyes from prey are other possibilities but, in the absence of data, aposematism seems the most applicable given that so many of these species have putrid gland secretions and formidable claws and teeth.

Aposematism cannot apply to all face masks, however (table 2). Several species of mouse possum (Marmosidae) have black or dusky brown markings around the eyes, as do the slow lorises (*Nycticebus*), the slender loris *Loris tardigradus* and dwarf lemurs (Cheirogaleidae). The feather-tailed possum *Distoechurus pennatus*, fork-marked dwarf lemur *Phaner furcifer* and douroucoulis or night monkeys (*Aotus*) have black or brown bands on muzzle, face or crown, and many small rodents have occular markings (e.g. garden dormice *Eliomys*). All of these are small nocturnal species relying on crypsis, so it is conceivable that reflected light off fur or skin could dazzle them at dawn and dusk. A similar argument might apply to three-toed sloths (*Bradypus*) that have dark eye patches set in a light face. Alternatively, face marks could function as signals of dominance or condition.

The giant panda has black eye spots set in a white face. These could conceivably be an anti-glare devices in snow.

Five families of primates exhibit a bewildering diversity of contrasting facial coloration: Lemuridae; Indriidae; Callithricidae; Cercopithecidae; and Hylobatidae (Bradley & Mundy 2008). Some species of lemur have prominent naked black muzzles or black fur surrounded by a white ruff, as in the black lemur *Eulemur macaco*, and subspecies of ruffed lemur *Varecia variegata variegata*, or surrounded by a crown of white hairs as in other subspecies of *Varecia variegata*, the indri *Indri indri* and sifakas (*Propithecus*). Some subspecies in *Eulemur* have dark faces with light patches above the eyes. The ring-tailed lemur *Lemur catta* has a white face with black eyes and muzzle. All of them are large (2–10 kg), diurnal, social and have conspicuous black and white bodies or tails (see below). Aposematism seems improbable given lack of obvious defences; large size makes relying on crypsis unlikely; and only black lemurs show sexual dichromatism (see electronic supplementary material). By elimination, therefore, face markings might serve in signalling to conspecifics; indeed, many lemurs including ruffed lemurs scent mark using chest, chin and neck secretions to rub the substrate (Pereira *et al.* 1988). An anti-glare function might possibly account for consistent black markings around the eyes.

All seven genera of Callitrichidae contain species with contrastingly coloured faces sometimes with elaborate moustaches, ear tufts or crowns. Emperor tamarins *Saguinus imperator* have black faces with a long white moustache and beard; cotton-topped tamarins *Saguinus oedipus* have a black head with white ear tufts and crown; the buffy-tufted-ear marmoset *Callithrix aurita* has a white forehead and ear tufts on a black face;

conversely, the black-tufted-ear marmoset *Callithrix penicillata* and Geoffroy's marmoset *Callithrix geoffroyi* have black ear tufts on a white face. There are many variations that incorporate patches of orange and brown fur. Callitrichids weigh less than1 kg are diurnal and live in small polyandrous family groups. Aposematism seems improbable given their palatability and lack of defences; crypsis might be aided by small size and greyish, brown coloured bodies but it is difficult to envisage brightly coloured faces contributing to background matching. Instead, intraspecific signalling, perhaps amplifying scent marking, seems a stronger candidate, although coloured facial adornments suggest sexual selection. As both sexes help raise offspring and reproductive suppression in both sexes is commonplace, mate choice in both sexes might be involved (Fernandez & Morris 2007).

Many species of Cercopithecine have strikingly coloured faces: the moustached guenon *Cercopithecus cephus* has a white moustache on a blue-black face; De Brazza's monkey *Cercopithecus neglectus* has a white beard too. Brows, cheeks and nasal spots are variously coloured white, black, red, yellow or blue. Most Cercopithecidae (3–12 kg) live in groups of 4–12 adult females with one breeding male, are arboreal and diurnal. They are preyed on by large raptors, chimpanzees *Pan troglodytes* and leopards *Panthera pardus* and defend themselves by flight, moving vertically through the canopy, and by mobbing. Aposematism and crypsis seem unlikely explanations for striking facial markings (although black, grey and silvery grey pelage may be difficult to see in the canopy), and visual amplification of scent marking seems improbable given its more limited role in guenon societies than in lemurs and callitrichids. Functional explanations for cercopithecoid faces are therefore difficult. A species isolation mechanism might be involved given so many guenons are sympatric in west and central African rainforests (the same argument applies to Neotropical callitrichids) but it seems extraordinary that coloration *per se* is required to distinguish conspecifics. Perhaps selection for crypsis is lessened for guenons and callitrichids living in the canopy and they can afford to be bright (Hershkovitz 1968)?

Other primates have black faces set in a white or light grey surround of fur, such as the grivet *Chlorocebus aethiops*, hanuman langur *Semnopithecus entellus* and guereza *Colobus guereza*. Gibbons (Hylobatidae) show a great diversity of face coloration with the common theme of black-skinned faces framed with a thin line of white fur outside of which fur is black, brown, orange or white. Most of the 11 gibbon species are allopatric, so facial differences may in part be attributed to genetic drift although the function of contrasting black and white faces of all these species is mysterious.

Turning to artiodactyls, all 6 species of Hippotraginae (e.g. gemsbok *Oryx gazella*) have light- or white-coloured bodies and faces with black wigs, cheek patches and patches between eyes and nostrils that may be joined depending on subspecies and individual; bontebok *Damaliscus pygargus* have a median stripe on a dark brown face. Again, explanations are difficult but artiodactyls with both black and white facial markings are diurnal and live in intermediate-sized groups, and species with conspicuous faces live in grassland or bushland habitats suggesting communication (Stoner *et al.* 2003*a*). Artiodactyls with white faces are found in open environments, however, suggestive of thermoregulation (Geist 1987). Blackbuck *Antilope cervicapra* have a white chin and eye rings contrasting with black or dark brown upperparts. Many artiodactyls have black or white eye rings (e.g. dik-dik *Madoqua kirkii*) or spots on their face (e.g. sao la *Pseudoryx nghetinhensis*) that probably draw attention to pre-orbital glands with which they scent and mark their territories. Possibly, the size or brightness of these may advertise ability to defend a territory?

Some rodents are a puzzle. Blesmols or African mole rats (Bathyergidae) are fossorial with poor vision but several species have white markings on their face or head. Are these used to signal dominance in dark underground tunnels or signal to conspecifics or predators in rare above ground forays? Both seem unlikely. The white and black facial bars of the plains viscacha *Lagostomus maximus* may be a candidate example of aposematic or pursuit deterrent signalling: this species can flee at 40 km h^{-1} with 3 m leaps and sharp turns.

(d) *Contrasting necks and chests*

Diverse taxa have conspicuous black and white neck markings (table 2). These include the black shouldered possum *Caluromysiops irrupta* with black shoulders and dorsal ridge on a grey body, the Tasmanian devil *Sarcophilus harrisii* with a small notch of white fur on a mostly black pelt, the Ryukyu flying fox *Pteropus tonganus* with a thick white necklace, European *Martes martes* and yellow-throated pine martens *Martes flavigula* with yellowish necks and chest patches, grison *Galictis vittata* with a black face and forelegs but white neck and forehead stripe, oriental civet *Viverra tangalunga* with three black and two white necklaces, and moon rat *Echinosorex gymnura* with white head and shoulders but black spots near the eyes. Some of these colour marks are probably aposematic; for example, the Malaysian civet is known for its pungent secretions and moon rats smell of onions and ammonia. Why these markings should be absent from face or dorsum is unknown.

Among ursids, the spectacled bear *Tremarctos ornatus* has large white circles around the eyes and a semicircle on the lower side of the neck on an otherwise black or dark brown body; their function is unknown. The Malayan sun bear *Ursus malayanus*, sloth bear *Ursus ursinus* and Asiatic black bear *Ursus thibetanus* all have prominent white chest marks on black bodies that, from their placement, signal dominance (table 1).

Neck markings could modulate intraspecific aggression by directing attention to the vulnerable neck area (the submissive 'gesture' could lessen the strength of attack, Tinbergen 1953; Lorenz 1966), but no experimental studies have been attempted. Neither has size nor brightness of neck or chest marks been correlated with dominance in mammals, although there are numerous avian examples of collars and chest badges signalling dominance (Ripoll *et al.* 2004; Senar 2006). Dominance of neck and chest marks should be explored in mammals.

(e) *Body with blocks of black and white fur*

A group of unrelated mammals sport blocks of black and white pelage: white head and neck set against a black torso (e.g. pied marmoset *Saguinus bicolour*, llama *Llama glama* and giant flying squirrel *Petaurista alborufus*); or black head and neck against a white trunk (e.g. Jentink's duiker *Cephalophus jentinki*). Others have a black body with white saddle such as the Malayan tapir or giant tree rats (*Mallomys*) or irregular large black patches on a white body including the black and white ruffed lemur and indri, or partially white body, the giant panda; or white shoulders on a black body as in the Angolan black and white colobus *Colobus angolensis*. The Sumatran short-eared rabbit *Nesolagus netscheri* has broad curving brown stripes over a grey body. Out of their natural environment, these species are highly conspicuous yet their coloration defies explanation. Aposematism is unlikely as none have obvious defences. Background matching seems improbable, given the majority live in tropical forests, although this is a remote possibility for the giant panda that seasonally occupies high elevation forests where dark shadow and melting snow may cover the ground (Loucks *et al.* 2003). In all of these species, most blocks of colour touch the animal's outline and are not internal to it; the borders of colour are perpendicular to the outline in the marmoset, panda, llama, duiker, tapir and flying squirrel, and they are always sharp. Disruptive coloration is therefore a possibility (table 1) at least in the solitary species, but why should it be so idiosyncratic? In social monkeys and llamas, conspicuous bodies may serve to communicate the presence to neighbouring groups in circumstances where visibility is obscured by trees or mist, or may amplify auditory or olfactory communication in lemurs and callitrichids, respectively, but this is all speculation (table 2).

A second group of unrelated species again have strong blocks of black and white fur but the former is on the dorsum and the latter is on the ventrum. These include the Herbert River ringtail possum *Pseudocheirus herbertensis* although it has black forelegs too; the cotton-top marmoset, although it has a white head; sable antelope *Hippotragus niger*, bontebok and blackbuck all of which have rich dark brown or black dorsal and lateral surfaces extending to a bright white ventrum; Prevost's squirrel *Callosciurus prevostii* and some populations of true lemmings (*Lemmus*). Coloration in these species does not gybe with design features of disruptive coloration because the border between black and white runs parallel to the body's outline, moreover most are group living. While a white ventrum speaks to countershading that might conceal shadow cast by the barrel of the body, one would expect a gradation of hue from dark to light as witnessed in many desert living bovids (Stoner *et al.* 2003*a*) rather than a sharp boundary. Perhaps a black dorsum absorbing heat and a white ventrum reflecting it allow some degree of behavioural regulation of body temperature, but this is guesswork. *Gazella* are a special case with four species having tan dorsa and white ventra separated by a broad black flank stripe that may be involved with intraspecific communication (Stoner *et al.* 2003*a*) or conceivably as amplifiers of manoeuvrability or aposematic reminders of flight speed?

(f) *Black body with white spots or blotches*

Many mammals have brown or grey coats with white spots: in carnivores, they are arboreal and may live in forests (Ortolani & Caro 1996); in young artiodactyls, these species are hidden after birth (Stoner *et al.* 2003*a*), each supporting pattern blending. Yet few mammals have black pelts with white spots. Exceptions are quolls (*Dasyurus*) with white blotches all over the body but not the tail; spotted cuscuses (*Spilocuscus*) with large black spots on white bodies; the uniquely spotted pinto bat *Euderma maculatum* with a white spot on each shoulder and one on its tail base; the spotted skunk with white blotches on a black coat and marbled polecat *Vormela peregusna* showing the converse; oriental linsangs (*Prionodon*) that have thick black or dark bands that traverse the back together with large lateral spots all on a whitish-grey background; and the black pacarana *Dinomys branickii* with two more or less continuous white lines near the midline of the back and two rows of white spots lower down on each side. Many of these species are variable in colour with brown replacing black.

Since all these species are solitary and nocturnal and can climb, pattern blending against patches of leafy shade seems the most obvious explanation for this coloration. Crypsis in the skunk and polecat raises an interesting issue, however, as they are also aposematic. If black and white coloration is normally a warning signal in mid-sized mammals, it could explain the absence of white spots on a black background in those mammals that need to be cryptic, and why white spots on a brown background are more common. Black and white coloration is not a combination that lends itself easily to pattern blending.

(g) *Trunk with black transverse stripes*

The numbat *Myrmecobius fasciatus* and three species of long-nosed bandicoots (*Parameles*) have transverse or diagonal dark and light bars on the back and rump; another marsupial, the extinct thylacine *Thylacinus cynocephalus* had 13–19 blackish brown transverse bands across the back, rump and base of tail. The banded palm civet *Hemilagus derbyanus* has broad transverse stripes along its back. Three species of zebra have transverse black and white stripes all over the body becoming horizontal on rump and legs. Grevy's *Equus grevyi* and mountain zebras *Equus zebra* have white unstriped bellies; Burchell's zebra shows shadow stripes between the main flank stripes in some populations; the extinct quagga *Equus quagga* (or *burchelli*) was striped on head and neck and anterior part of the body. The striped-back duiker *Cephalophorus zebra* has dark vertical stripes on a bright orange coat with white or dark underparts.

How can we explain these patterns? In carnivores, vertical stripes of differing colours are associated with grassland habitat and terrestrial locomotion (Ortolani 1999; but see Ortolani & Caro 1996), and in artiodactyls striped species live in woodlands and open forest, and striped young are hidden after birth (Stoner *et al.* 2003*a*) all indicative of pattern blending (table 2). This might apply to the marsupials, palm civet and duiker that live in forested habitats and that are terrestrial but why do so few members of their

Table 2. Summary of conclusions reached in the text.

categories taxon	principal function of white and black pelage[a]	likelihood[b]
(*a*) *black and white quills*		
echidnas	aposematism	likely
tenrecs[c]	aposematism	likely
hedgehogs	aposematism	likely
new world porcupines	aposematism	very likely
old world porcupines	aposematism	very likely
(*b*) *horizontal white dorsal fur*		
mephitids, mustelids[c], herpestids[c]	aposematism	very likely
striped possums[c]	aposematism	likely
anteaters[c]	aposematism	possible
(*c*) *black and white face masks*		
canids[c], procyonids[c], mustelids, mephitids, viverrids[c]	aposematism	likely
possums[c], dwarf lemurs[c] and three-toed sloths	anti-glare	best guess
lemurs[c]	conspec signals	best guess
callitrichids[c]	sexual signals	best guess
guenons[c]	—	unknown
old world monkeys[c], gibbons	—	unknown
artiodactyls[c]	conspec signals or thermoregulation	possible best guess
(*d*) *contrasting necks or chests*		
gymnures[c], mustelids[c], viverrids[c]	aposematism	likely
various species (e.g. Ryukyu flying fox)	—	unknown
ursids[c]	dominance badges	best guess
(*e*) *body with blocks of black and white fur*		
various solitary species (e.g. Malayan tapir)	disruptive	best guess
various social species (e.g. b&w colobus, gazelles)	conspec signals	best guess[d]
various species with horizontal border (e.g. blackbuck)	—	unknown
(*f*) *black body and white spots or blotches*		
various species (e.g. quolls)	pattern blending	likely
(*g*) *trunk with black transverse stripes*		
marsupials[c], carnivores[c], duikers[c]	pattern blending	best guess
zebras	—	unknown
(*h*) *contrasting feet, legs and rumps*		
feet: kangaroos[c], primates[c]	non-functional	best guess
legs: carnivores[c]	aposematism	best guess
legs: bovids[c]	conspec signals	possible
rumps: artiodactyls[c]	signals[e] or thermorgn	possible
(*i*) *black and white tails*		
ringed tails: primates[c] carnivores[c]	conspec signals	likely
ringed tails: carnivores[c]	aposematism	best guess
white tails: carnivores[c]	aposematism	likely
white tail tips: many species (e.g. elephant shrew)	lures[f]	possible
black tail tips: many species (e.g. springhare)	conspec signals	best guess
(*j*) *all white*		
carnivores[c]	background matching or thermoregulation	likely[g] possible
artiodactyls[c]	background matching or thermoregulation	likely[g] possible
marsupials[c], sifakas[c]	—	unknown
(*k*) *sexual dichromatism*[h]		
pelage: lemurs[c], gibbons[c]	intrasexual competition	possible
ornaments: various species (e.g. lion)	inter/intrasexual competition	possible
genitalia: baboons[c], managabeys[c], macaques[c]	intrasexual competition	possible

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[a] Refers to function most likely to influence fitness but other functional consequences may apply.

[b] Very likely: no alternative hypothesis can explain distribution of the coloration across species but still not tested systematically. Likely: best hypothesis but others cannot be dismissed. Possible: based on indirect supporting evidence only. Best guess: alternative hypotheses could apply and no systematic tests carried out. Unknown: no hypothesis stands up to scrutiny.

[c] Only some species in the family exhibit the coloration.

[d] Best guess for colobus, but gazelles: possible.

[e] Signalling to predators or conspecifics.

[f] Carnivores.

[g] Particularly arctic species.

[h] See electronic supplementary material.

clades, and mammals in general, show this form of coloration? Again, juxtaposition of black and white may not lend itself to crypsis.

Zebras are more problematic (Ruxton 2002) because they spend much time in open environments, making background matching or pattern blending unlikely. Despite stripes not following the body's outline, their regularity speaks against disruptive coloration and leans towards aposematism, yet their defences are limited to forceful bites ands kicks. This has led to some bizarre hypotheses such as stripes setting up convection currents that cool the animal (Kingdon 1979), avoidance of tsetse flies *Glossina* sp. (Waage 1981), predator confusion (Kruuk 1972) and facilitation of affiliative interactions (Kingdon 1984). At present, the function of zebra stripes is unsolved.

(h) *Contrasting feet, legs and rumps*

Leg coloration contrasting with the body is uncommon in mammals. Black hands and feet are seen, however, in Lumholtz's tree kangaroo *Dendrolagus lumholtzi*, the swamp wallaby *Wallabia bicolour* and some large *Macropus*; in the ruffed lemur, indri and hanuman langur. In some sifakas, De Brazza's monkey and Douc langur *Pygathrix nemaeus* and some snub-nosed monkeys (*Rhinopithecus*) black pelage extends up to the forearms. The red fox *Vulpes vulpes*, raccoon dog, maned wolf, black-legged mongooses (*Bdelogale*) and white-tailed mongoose all have black legs. Selous's mongoose *Paracynictis selousi* has black feet, and the black-footed cat *Felis nigripes* walks on its toes exposing its black paws! The yellow-handed marmoset *Saguinus midas* has yellow hands and feet.

Extremities in mammals are cooler than core body temperatures, consequently hair follicles become melanistic (Hamilton 1973). This might explain black hands and feet in kangaroos and primates, and perhaps even red fox and maned wolf. Black legs in white-tailed and Selous's mongooses probably signal aposematism but this is not established in black-legged mongooses.

It is only among Bovidae where contrasting leg coloration is commonplace. Here, members of some genera have white legs (*Capra*, *Pseudovis*), or white stockings (*Bos* and *Ovis*, along with the bontebok, gemsbok and goral *Naemorhedus goral*); or white spots on the fetlocks (*Kobus* as well as nilgai *Boselaphus tragocamelus*, Derby's eland *Taurotragus derbianus* and sao la *Pseudoryx nghetinhensis*) or elsewhere on the shank (e.g. tahr *Hemitragus hylocrius*). Other species show black frontal surfaces on the forelegs (*Kobus*, *Capra*, *Pseudovis* along with the chiru *Pantholops hodgsonii*); or black upper legs (e.g. hartebeest *Alcelaphus buselaphus*, gemsbok, blackbuck); or black stockings (a few *Cephalophus*); or black spots on the fetlocks (nilgai, Derby's eland, impala *Aepyceros melampus*) or elsewhere on the leg (e.g. eland *Taurotragus oryx*).

Leg coloration has been scrutinized in artiodactyls (Stoner *et al.* 2003*a*). Dark legs are seen in desert living species and those in large social groups, white legs in diurnal species and additionally species that live in either grassland or bushland habitats, or both: all suggesting communication. Some white and black spots are positioned over scent glands, as on fetlocks, so perhaps amplify olfactory signals (table 2). Little else is known, however, and placement of leg patches has not been investigated.

Certain artiodactyls have contrasting rumps (Guthrie 1971*a*), notably the okapi *Okapi johnstoni* with its horizontal black stripes that extend from the rump to half way down the hindlegs (and on the forelegs). Conspicuous white rumps are found in assorted deer (Cervidae), white-tailed deer *Odocoileus virginianus* being a prime example, some *Bos*, *Cephalophus* and *Kobus* species, all the gazelles, and most of *Capra* and *Ovis*. Artiodactyls with white rumps are usually diurnal, live in large groups, in open habitats, principally in deserts, and may be pursued by coursing predators (Stoner *et al.* 2003*a*). These analyses support a role in communication to conspecifics, or even to predators, but also thermoregulation if the rump is turned to reflect sunlight (Bicca-Marques & Calegaro-Marques 1998).

(i) *Black and white tails*

Tails with repeated rings of black and white fur are exhibited by the ring-tailed lemur, some species of callitrichid such as the buffy-tufted-ear marmoset and Geoffroy's marmoset; and many carnivores including the ringtail *Bassariscus astutus*, raccoons (*Procyon*), coatimundis (*Nasua*), oriental civets (*Viverra*), rasse *Viverricula indica*, genets (*Genetta*), African linsang *Poiana richardsoni*, oriental linsangs (*Prionodon*), small felids including the little spotted cat *Felis tigrina* and Geoffroy's cat *Felis geoffroyi* and some of the larger cats including cheetah *Acinonyx jubatus*. Certain squirrels in the (*Epixerus*, *Heliosciurus*) have ringed tails, and several jerboa genera (Dipodidae) have black and white tufted tails.

It is exceedingly difficult to explain such variety and many functional explanations must be involved (Kiley-Worthington 1976) (table 2). For example, ring-tailed lemurs rub fatty secretions on to their tails, erect them during intergroup encounters and thereby disperse their scent (Drea & Scordato 2007), so do ruffed lemurs; here, conspicuous tails probably amplify olfactory signals (Richard 1985). Tail bands in marmosets and squirrels might mediate intraspecific communication too. Ringtails discharge noxious anal secretions when alarmed. More systematically, yet mysteriously, ringed tails in carnivores are associated with a nocturnal and arboreal lifestyle, and living in closed habitats and forests (Ortolani 1999). It is worth noting, however, that tail banding is reminiscent of repetitive colours in aposematic snakes and caterpillars, and secondly, that it may result from developmental constraints in otherwise spotted species (Murray 1981; but see Ortolani 1999).

A great many mammals have conspicuous white tips or terminal segments to their tails including but not limited to the four-eyed *Philander opossum*, water *Chironectes minimus* and striped possum *Dactylopsila trivirgata*; prosperine rock wallaby *Petrogale persephone*, rabbit-eared bandicoot *Macrotis lagotis*, pen-tailed tree shrew *Ptilocercus lowii*, Angolan black and white colobus, maned wolf, African hunting dog *Lycaon pictus*, white-tailed mongoose, white-tailed deer, west African brush-tailed porcupine *Atherurus africanus* and golden rumped elephant shrew *Rhynchocyon cirnei*. A number of murids have naked white distal sections to their tails: *Cricetomys*; *Uromys*; *Leptomys*; and *Paraleptomys*.

Black tail tips are found in the kowari *Dasyuroides byrnei*, brush-tailed possum *Trichosurus vulpecula*, ruffed lemur, squirrel monkeys (*Saimiri*), lion *Panthera leo*, ermine *Mustela erminea*, Owston's palm civet *Chrotogale owstoni*, eland, long-eared jerboa *Euchoreutes naso*, slender-tailed cloud rats (*Phloeomys*), springhare *Pedetes capensis* and black-tailed jackrabbit *Lepus californicus* to name only a sample.

White tails in mustelids and herpestids are associated with producing noxious anal secretions (Ortolani & Caro 1996), and white tails in striped possums, mephitids and porcupines surely signal aposematism.

White tail tips occur in grassland carnivores, in species that prey on birds and small mammals, whereas black tails are seen in diurnal, grassland, terrestrial and small carnivore species and those that prey on small mammals and ungulates (Ortolani 1999). These findings are consistent with carnivores either luring prey (Estes 1991) or distracting prey from recognizing the predator. White tail tips are also found in carnivores preyed upon by raptors (Ortolani 1999) and add weight to an experiment that showed that red-tailed hawks *Buteo jamaicensis* deflect their attack to the tail tip of moving weasel models rather than to the body (Powell 1982). Conceivably, deflection might be the function of contrasting tail tufts at the end of jerboas' long tails? In artiodactyls, conspicuous tail tips are associated with being diurnal and gregarious (Stoner *et al.* 2003*a*), and contrasting tail tips are similarly associated with sociality in lagomorphs (Stoner *et al.* 2003*b*) both of which imply intraspecific communication. These broad scale analyses have been conducted on only a few orders so far and are not sufficiently sophisticated to narrow alternative hypotheses that include pursuit deterrence amplifiers, species recognition markers, signals for helping conspecifics follow, courtship, or mechanical constraints limiting tail hairs to certain colours.

(j) *White mammals*

Albinism aside, rather few mammals sport all white pelage except the greater glider *Petauroides volans*, silky anteater *Cyclopes didactylus*, ghost bats (*Diclidurus*) and some sifakas (*Propithecus*) although individual variation is great; polar bear *Ursus maritimus* year round; and Arctic fox *Alopex lagopus*, ermine *Mustela erminea*, least weasel *Mustela nivalis*, long-tailed weasel *Mustela frenata* and Arctic hare *Lepus arcticus* that all turn white in winter (although the ermine retains its black tail tip). Many artiodactyls take on lighter coats in winter (Cott 1940) and some are white all year (e.g. North American mountain goat *Oreamnos americanus*, mouflon *Ovis orientalis* and Dall's sheep *Ovis dalli*). Several desert living species have tan coats verging on white, such as the fennec *Vulpes zerda*, addax *Addax nasomaculatus* and antelope jackrabbit *Lepus alleni*. Some mammals have polymorphic white forms such as the marsupial mole *Notoryctes typhlops*, spotted cuscus, black bear *Ursus americanus* (Rounds 1987) or human *Homo sapiens*.

The silky anteater is a possible case of masquerade in mammals. Nocturnal, it is found in *Ceiba* trees and is similarly coloured to silverfish fibrous seed pods. Carnivores that are either permanently or seasonally white are found in Arctic and tundra habitats (Ortolani & Caro 1996). Similarly, there is a strong association between artiodactyls taking on lighter coats in winter and occupying tundra and Arctic regions (Stoner *et al.* 2003*a*), but the relative importance of crypsis against white snow or thermoregulation is unclear (Russell & Tumlison 1996). There is debate as to whether air within the lumen of white hairs causes the fibre to behave optically and help heat skin below (Grojean *et al.* 1980; Koon 1998). Hair insulation properties additionally depend on number, length, diameter and angle of hairs. Wallace (1879) argued that because species not relying on concealment do not change colour in winter (consider musk oxen *Ovibos moschatus* that circle against wolves *Canis lupus*), white must be a form of camouflage. Moreover, birds and mammals with seasonal colour change occupy backgrounds appropriate to their hue (Litvaitis 1991; Steen *et al.* 1992) and even dirty themselves (Montgomerie *et al.* 2001) again supporting crypsis.

In carnivores, pale coats are associated with living in desert or semi-desert environments (Ortolani & Caro 1996) and in lagomorphs with tundra and barren land (Stoner *et al.* 2003*b*) although, surprisingly, not in artiodactyls (Stoner *et al.* 2003*a*). The relative import of reflecting heat and crypsis in these environments is opaque too (table 2).

4. DISCUSSION

Black and white coloration is not the only form of conspicuous coloration in mammals: there are eye-catching species with red, yellow, brown and grey pelage such as the Huon tree kangaroo *Dendrolagus matschiei*, yellow-footed rock wallaby *Petrogale xanthopus* and douc langur *Pygathrix nemaeus*. Furthermore, in some species one sex is conspicuous but the other not (electronic supplementary material). Moreover, contrasting coloration apparent in zoo or museum specimens may not be as conspicuous under natural conditions (Wallace 1889; Poulton 1890; Thayer 1909; Hingston 1932). These limitations notwithstanding, I will attempt to generalize about the evolution of contrasting coloration in a class recognized as being drab compared with birds and insects.

Different areas of the body are either viewed principally by conspecifics, prey or predators, from near or from afar, or are exposed to the sun or hidden, each of which sets up different selection pressures. Aposematic defences require a signal that predators recognize up close so we might expect (i) contrasting colours to be seen nearby but not at a distance, as in hedgehog quills, (ii) for the signal to direct the predator's attention to the defence itself (e.g. possibly giant anteater claws), and (iii) the signal to be the most prominent on the dorsum in species that are attacked by larger predators towering over them (e.g. white-tailed mongoose; but see Donaldio & Buskirk 2006). These ideas are broadly supported by the evidence although mephitids can be seen at a distance by humans.

Areas of the face, neck and chest are most likely viewed up close by conspecifics so we would expect contrasting colours there to be involved principally in intraspecific communication, all the more so in social species. Visual signals used in competitor assessment (e.g. badges on the chest, markings that attract attention to teeth, Guthrie 1971*a*,*b*) or in mate choice (e.g. health indicator markings) need not be seen from far away and can be limited in size and conspicuousness. In circumstances in which a predator is confronted over food, or rests in a burrow or tree hole, warning signals might be expected on its face and neck. Anti-glare devices may be expected around the eyes.

Large blocks of colour on the torso suggest either intraspecific signals that must be perceived at a distance, perhaps in territorial species; or, in solitary species, pattern blending against bright sky or snow and dark shadow, or disruptive coloration. Some of the best known mammals with black and white fur fall into this category: indris, black and white colobus, giant pandas and Malayan tapirs but until difficult field experiments are conducted it is unlikely that these hypotheses can be tested with rigour.

In species without defences, and that therefore need to be cryptic to predators at both distance and nearby, colours that match a uniform background or blend in with the pattern of light cast by vegetation need to encompass the whole body. This is seen in species with entirely white pelage, species with white spots or blotches covering a black body and perhaps some species with transverse stripes.

Depending on the body form of a species, legs and rumps may be seen easily at a distance or else hidden. In taxa where the trunk is high off the ground, legs might signal to conspecifics, particularly the front of the forelegs during contests or courtship displays. In species that do not rely on crypsis and that additionally signal unprofitability to predators, signals might be expected on the distal surfaces of hindlegs or on the rump. Fur coloration can vary with condition in at least one mammal (West & Packer 2002). Alternatively, patches simply serve as a reminder of a species' flight speed. Hands and feet in many species are subject to temperature extremes that may drive their coloration.

We might expect tail coloration to serve several functions because a tail can be voluntarily displayed or hidden. It might reify aposematic coloration elsewhere on the body, expose or conceal a colour patch (as in artiodactyls rumps), or signal alarm (Stankowich 2008), arousal or dominance to conspecifics, distract predators or prey or even signal unprofitability to predators (table 1). Tails, therefore, may be the most difficult area of the body in which to investigate the adaptive significance of coloration.

5. CONCLUSIONS

Aposematism apparently evolved several times in mammals, in Monotremata, Xenartha, Insectivora, Carnivora and Rodentia. It can be expressed on the body, especially as white hair on the dorsum and tail, and as black and white marking on the face and neck. These species constitute the most definitive examples of the functional significance of coloration in mammals, although experimental tests are lacking.

Conspicuous coloration may mediate intraspecific communication in several primates (lemurs, callitrichids, colobines), carnivores and artiodactyls but the nature of the evidence is far less compelling than for warning signals, and the type of information conveyed and to what audience is hardly known. Sexual dichromatism is a strong example of signalling to conspecifics but it is unknown whether dark coloration in males (electronic supplementary material) has been driven by male–male competition or female choice, and what factors limit the extent of sexual dichromatism.

Arguably, crypsis is poorly served by contrasting black and white coloration patterns except against snow or forests with patches of light and dark. Currently, there is no firm evidence for disruptive coloration in mammals.

It is still a large and open question as to the role that white pelage plays in absorbing or reflecting heat in Arctic environments, reflecting heat in desert environments and in insulation. Evidence that black areas around the eyes reduce glare and that tail tips lures are suggestive only at the best. Finally, the staggering variety of patterns of coloration across mammals, particularly in two primate families, between populations, and among individuals intimates greater lability than many other morphological traits and forces us to consider non-adaptive explanations for coloration in some members of this class.

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