

The function of facial masks in “midguild” carnivores

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A group of medium sized carnivores possesses conspicuously colored facial markings or masks. This facial coloration is most compatible with the aposomatic warning hypothesis and functions to deter predation by larger carnivores. Other hypotheses addressing ecological or social functions are not supported by the data. Facial masks may be a recent character derived from an ancestral contrast in body coloration of carnivores that functioned to warn potential predators of a disproportionate danger in attacking the smaller guild member. This danger may be predicated either on the relative ferocity of the smaller carnivore (wolverine/badger-type) or that the smaller carnivore is equipped with a defensive nauseous discharge that is directly harmful to larger would-be predators. Facial masks in themselves appear to function as an aposomatic warning of aggressive defensive behavior that could be harmful to predators.

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Coloration in mammals is limited to various shades of browns and tans to grays and blacks and whites with infrequent highlights of reds, yellows or blues in a few primates. In general, coloration in mammals appears to follow Gloger’s rule with darker colors in riparian habitats and lighter colors in open areas providing appropriate camouflage and protective coloration as well as thermoregulation to absorb or repel heat, respectively (Cott 1940, Hamilton 1973). However, some species of mammals have distinct contrasts in markings, such as in the face and head region of some ungulates and primates (Guthrie and Petocz 1970), white rump patches (Guthrie 1971) and light and dark bands on legs, faces, and rumps (Geist 1978, 1987). These markings and color contrasts may serve as horn mimics (Guthrie and Petocz 1970), to attract attention to scent glands (Kitchen and Bromley 1974), interspecific anti-predator warnings (Wickler 1968, Rowland 1979, Caro 1986, FitzGibbon and Fanshawe 1988), appeasement signals (Guthrie 1971), or as general threat displays

(Guthrie and Petocz 1970, Geist 1978). The majority of literature discussing coloration in mammals has focused on ungulates and colors associated with behavioural communication or ecological phenomena (Stoner et al. 2003).

Coloration in carnivores has received less attention, especially as it relates to distinct and conspicuous markings in the facial region (but see Ortolani and Caro 1996, Ortolani 1999). Concealment, communication and regulation of physiological processes are generally proposed as the basis underlying the evolution of color patterns in mammals (Cott 1940, Ortolani and Caro 1996, Ortolani 1999). Ortolani and Caro (1996) report on a comparative analysis, controlling for phylogenetic relationships, of differences in the appearance of pelage across the Carnivora. They found that pale coats are associated with living in deserts, dark coats with living in tropical forests and white coats with arctic conditions. Spotted carnivores tend generally to be arboreal, while spotted felids, specifically, are usually

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forest dwellers. Intriguingly, their study could not detect any significant relationship between striped pelage and grassland habitats, or between sociality and contrasting throat patches, ear marks, or tail tips. This negative result challenges prevailing wisdom that has assumed a functional association between these traits.

One aspect of coloration that has not been comprehensively addressed in carnivores is the conspicuous contrast in facial coloration referred to here as facial “masks” (Fig. 1). Although most mammals, including carnivores, appear to have dichromatic color vision, patterns of contrasting brightness in the pelage, regardless of hue and chroma, can even be perceived with monochromatic vision, making these patterns particularly useful in low-light conditions (Jacobs 1993). Previous discussions on mammalian coloration patterns have not proposed a functional or evolutionary explanation for these conspicuous facial markings or contrasting color masks.

In general, carnivore guilds often involve three species scales, one large (>30 kg) and mainly carnivorous (e.g. gray wolf *Canis lupus*, brown hyena *Parahyaena brunnea*, jaguar *Panthera onca*) one medium-sized (10–20 kg) and often omnivorous (e.g. American badger *Taxidea taxus*, ratel *Mellivora capensis*, coati *Nasua nasua*) and another small and usually predatory (e.g. ermine *Mustela erminea*, American mink *Mustela vison*, foxes e.g. *Vulpes vulpes*) (Johnson et al. 1996). These patterns arise from the rules of community assembly, which are posited to be associated with character displacement (Dayan et al. 1991). As it turns out, masks occur predominantly in a select group of typically medium sized “midguild” mammalian carnivores, which have the distinction of co-existing in the presence of larger carnivores. However, these midguild carnivores retain the capacity (ferocity/scent defenses) to do harm to, or deter predatory advances from the carnivore competitor immediately above them on a higher tier of their local guild. Herein we present the hypothesis that the functional significance of facial masks in these “midguild” carnivores is for aposematic coloration as a warning to deter predation from larger carnivores.

Methods

Facial markings consist primarily of a dark band of pelage that extends from the sides of the face across the eyes and rostrum of the nose. Although the patterns of these markings vary, they typically resemble a “bandits” mask covering the eyes or eye-like schemata (Fig. 1). These masks vary in intensity between species, but in all cases possess sufficient aposematic contrast to function as a visual cue or flag, especially in low light scenarios. Based on the text, photos, and illustrations in Prater

(1971), Nowak (1999), and Macdonald (2001) we identified 36 species from four families of Carnivora, the Mustelidae, Procyonidae, Canidae and Viverridae that have facial masks (Table 1). We also provide data on the 75 other species from these families that do not have masks.

Hypotheses examined

The following hypotheses have been proposed or suggested previously in the literature, or have been developed from our own reading and understanding of mammalian behavioral ecology. Previous investigations have not cross-evaluated the varied hypotheses proposed for the evolution of masks, as we do here.

Eye patches and eye contour banding may act as an anti-glare device?

Ortolani (1999) proposed that dark eye patches might reduce the visual glare, especially in riparian habitats, in much the same way that football players use dark paint under the eyes when playing on bright days and inuits rub soot around their eyes to prevent snow blindness (Densley 1979). Eye patches have been found to function in this way for some gull species (Densley 1979). However, Ortolani (1999) found no association between nocturnal or diurnal activity, or for closed or open habitats, with regard to eye patches. Many of the species with masks are forest-dwelling and (or) nocturnal and thus would not be exposed to bright light. Consequently, this hypothesis does not seem to be a plausible explanation for facial masks in this unique group of carnivores. Also, this hypothesis does not explain why the other 75 species in these families do not have facial masks.

Conspicuous coloration may help to advertise an individual's location or to maintain group cohesiveness (Rowland 1979)?

The majority of the masked mid-guild carnivores listed in Table 1 are asocial and thus maintenance of group cohesion or use of facial markings for social communication is unlikely. The carnivores that possess facial masks, as well as other carnivores without masks, communicate primarily through olfactory means (Gosling and Roberts 2001, Buesching et al. 2002). Some of the social ungulates and primates may use facial coloration and displays for establishing dominance or maintaining hierarchies (Guthrie and Petocz 1970, but see Stoner et al. 2003), whereas these same patterns and arguments do not appear relevant for carnivores (Ortolani 1999) or for the select



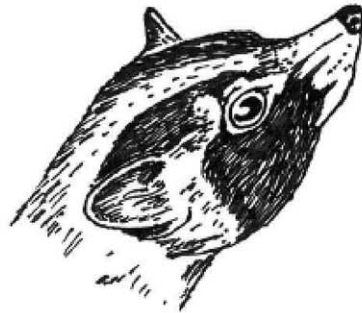
American Badger *Taxidea taxus*



Eurasian Badger *Meles meles*



Marbled Polecat *Vormela peregusna*



Palm Civet *Paradoxurus hermaphroditus*



Raccoon *Procyon lotor*



Raccoon Dog *Nyctereutes procyonoides*



Striped Skunk *Mephitis mephitis*



Wolverine *Gulo gulo*

Fig. 1. Illustrations of midguild carnivores with conspicuous facial markings.

Table 1. Representative species from four families of mammals that do and do not have facial masks, their body mass, habitat, and potential predators.

| Family, Species | Body mass, kg | Facial mask | Habitat | Potential predators |
|---|---------------|-------------|---|---|
| Mustelidae | | | | |
| European polecat, <i>Mustela putorius</i> | 1.4 | Yes | Forest | Wolf <i>Canis lupus</i> , lynx <i>Lynx lynx</i> , raccoon dog <i>Nyctereutes procyonoides</i> , raptors, red fox <i>Vulpes vulpes</i> |
| Marbled polecat, <i>Vormela peregusna</i> | 1 | Yes | Steppe, semi-desert grassland | Wolf, red fox, lynx, raptors |
| Steppe polecat, <i>Mustela eversmannii</i> | 2 | Yes | Steppe, semi-deserts | Wolf, red fox, lynx, raptors |
| Siberian weasel, <i>Mustela sibirica</i> | 0.8 | Yes | Tundra, steppe | |
| Black-footed ferret, <i>Mustela nigripes</i> | 1 | Yes | Prairie grasslands | Coyote <i>Canis latrans</i> , raptors, wolf |
| Grison, <i>Galictis vittata</i> | 2–3 | Yes | Semi-arid regions, open shrub grassland | Golden jackal <i>Canis aureus</i> , cheetah <i>Acinonyx jubatus</i> , hyena sp, e.g. <i>Hyaena hyaena</i> , <i>Parahyaena brunnea</i> , <i>Crocuta crocuta</i> , lion <i>Panthera leo</i> |
| Patagonian weasel, <i>Lyncodon patagonicus</i> | 1 | Yes | Pampas, grassland shrub | Jaguar <i>Panthera onca</i> , maned wolf <i>Chrysocyon brachyurus</i> , grey fox <i>Urocyon cinereoargenteus</i> , pampas cat <i>Lynchailurus pajeros</i> , raptors |
| North African striped weasel, <i>Poecilictis libyca</i> | 0.25 | Yes | Grassland, semi-desert | Golden jackal, caracal <i>Felis caracal</i> , raptors |
| Wolverine, <i>Gulo gulo</i> | 10–15 | Yes | Tundra, shrub, taiga forests | Bears e.g. <i>Ursus arctos</i> , <i>Ursus maritimus</i> , <i>Ursus americanus</i> , wolf, cougar <i>Felis concolor</i> |
| European badger, <i>Meles meles</i> | 8–12 | Yes | Forest edge, grassland, shrub | Wolf, lynx, bears |
| Honey badger (ratel), <i>Mellivora capensis</i> | 8–12 | Yes | Open dry savannah to dense forest | Jackal, raptors, lions cheetah, hyena, wild-dog <i>Lycaon pictus</i> |
| Teledu, <i>Mydaus javanensis</i> /Palawan stink badger, <i>Mydaus marchei</i> | 2–4 | Yes | Mountains SE Asia | Dhole <i>Cuon alpinus</i> , dingo <i>Canis dingo</i> , leopard <i>Panthera pardus</i> , tiger <i>Panthera tigris</i> |
| Hog badger, <i>Arctonyx collaris</i> | 7–14 | Yes | Forests SE Asia | Dhole, tiger, leopard |
| Ferret badgers, <i>Melogale</i> (4 species) | 2 | Yes | Grasslands, shrublands | Leopard, tiger |
| American badger, <i>Taxidea taxus</i> | 4–12 | Yes | Grasslands, open habitats | Coyote, wolf, bears, cougar |
| Martens, <i>Martes</i> (7 species) | 1–2 | No | Arboreal, forests | Bobcat <i>Lynx rufus</i> , lynx, coyote, wolf, raptors, larger felids, |
| Fisher, <i>Martes pennati</i> | 2–5 | No | Forests, | Bobcat, lynx, wolf, bears, cougar |
| American mink, <i>Mustela vison</i> | 1–1.5 | No | Aquatic, riparian | Foxes, raptors, wolf, coyote, bobcat, |
| Tayra, <i>Eira barbara</i> | 4–6 | No | Forest, C. S. America | Jaguar |
| Otters, (13 species) | 5–30 | No | Aquatic | Few terrestrial predators due to aquatic habitat |
| Weasels, <i>Mustela</i> spp | <0.4 | No | Terrestrial, forest, grassland | Hawks, owls, foxes, larger mustelids, bobcat |
| Procyonidae | | | | |
| Raccoon, <i>Procyon lotor</i> | 5–8 | Yes | Riparian, forest, woodland | Bobcat, coyotes, bears, wolves, lynx, cougar |
| Other racoons <i>Procyon</i> (6 similar species) | 3–8 | Yes | Riparian, forest, woodland | Jaguar, ocelot <i>Leopardus pardalis</i> , coyote, other felids |
| Ringtailed coati, <i>Nasua nasua</i> | 4–5 | Yes | Forest | Ocelot, jaguar, zorros <i>Dusticyon</i> sp. |
| Red panda, <i>Ailurus fulgens</i> | 3–5 | Yes | Bamboo forests | Tiger |
| Ringtail, <i>Bassariscus astutus</i> | 1 | Yes | Dry, open rocky cliffs, desert, shrub | Bobcat, raptors, cougar, black bears, wolves |
| Cacomistle, <i>Bassariscus sumichrasti</i> | 1 | Yes | Dry forest, savannah, desert shrub | Bobcat, raptors, ocelot, cougar |
| Kinkajou, <i>Potos flavus</i> | 2–5 | No | Arboreal | Zorros, ocelot, jaguar, alligator <i>Alligator</i> sp. |
| Canidae | | | | |
| Raccoon dog, <i>Nyctereutes procyonoides</i> | 8–12 | Yes | Woodland forest | Tiger, leopard |
| Bat-eared fox, <i>Otocyon megalotis</i> | 3–4 | Yes | Grassland, open savannahs | Cheetah, hyena, |
| Other foxes (3 genera, 23 species) | 2–5 | No | Grassland to forest | Numerous canids and felids |
| Viverridae | | | | |
| African civet, <i>Civetticus civetta</i> | 7–20 | Yes | Savannahs, grassland, forest-shrublands | Jackal, raptors, lion, cheetah, hyena, leopard |

Table 1 (Continued)

| Family, Species | Body mass, kg | Facial mask | Habitat | Potential predators |
|--|---------------|-------------|---|--|
| Common palm civet, <i>Paradoxurus hermiphroditus</i> | 3–4 | Yes | Tropical forests | Tiger, leopard |
| Masked palm civet, <i>Paguma larvata</i> | 4–5 | Yes | Forests and brush | Tiger, leopard |
| Banded palm civet, <i>Hemigalus derbyanus</i> | 2–3 | Yes | Tropical forests | Tiger, leopard |
| African civet, <i>Civettictis civetta</i> | 13 | Yes | Grasslands, open habitats | Jackal, raptors, lions, cheetah, hyena, wild-dog |
| Other civets and genets 33 species | 2–13 | No | Forest to grassland, most are semi-arboreal | Jackal, raptors, lions, cheetah, hyena, wild-dog |

group of asocial midguild carnivores with masks (this paper).

Coloration may serve to orient the bites of conspecifics during play, or ritualised fighting to areas where the skin is tough (Vemmer and Scow 1977)?

In low light scenarios, should an intraspecific agonistic encounter occur, then the pattern of coloration on the opponent's head and body may provide immediate cues about orientation and appropriate bite–strike areas. Dark patches may disguise the eyes in aggressive encounters, or serve to highlight an area to be avoided in ritualistic play. However, many other cryptically marked midguild carnivores also engage in intraspecific fighting without the need for facial markings (e.g. foxes, martens, otters) so this hypothesis seems unlikely.

Are facial markings a cue to elicit grooming by conspecifics?

Kleiman (1967) suggested that the facial markings of bat-eared foxes (*Otocyon magalotis*) and raccoon dogs (*Nyctereutes procyonoides*) may be a visual cue for grooming. Bat-eared foxes are relatively social and grooming is common, but many of the masked species are asocial and allo-grooming is probably uncommon. Also, facial grooming is common in all species of social carnivores, most of which do not have conspicuous facial markings. Thus, it is unlikely that masks have evolved as a social cue for grooming.

Do conspicuous markings serve in mate choice as a result of sexual selection?

There is no a priori reason to predict why facial markings should occur in some midguild carnivores and not others. Also, the facial masks described here occur during early ontogeny and even at birth in some species (Neal 1990), rather than at the time of sexual maturation. In addition, sexual selection can often canalize or reduce variation in traits associated with mate preferences (Cahalane 1958, Prater 1971, Ewer 1973); whereas coloration, size, and placement of face masks show considerable variation within species. A general visual cue such as black and white as in skunks, or dark bands across the eyes as in racoons, civets, polecats and others could likely serve as aposematism (discussed below), but is not likely a sexually selected trait.

Coloration is used to enhance the apparent size of teeth or body (Pruitt and Burghardt 1977) which may be exaggerated with piloerection, tail-raising, bipedal standing and other displays?

This hypothesis is not mutually exclusive of our proposal that aposematic coloration in midguild carnivores serves as an antipredator warning. The placement of the facial coloration across the eyes, however, is in contrast to what would be expected if coloration were to enhance the size or weaponry or fighting ability (Guthrie and Petocz 1970). Also, many carnivores including other medium-sized ones without facial masks or conspicuous markings (e.g. otters, fishers *Martes pennanti*, foxes) have well developed teeth for attack and defence yet fight in similar ways to midguild carnivores with masks. Therefore, we see no obvious relationship between the presence of masks and any aspect of weaponry.

Do facial markings provide crypsis/disruptive coloration and make the masked carnivores less conspicuous?

Ortolani (1999) established no association between dark markings around the eyes and camouflage. Crypsis and face masks would appear to be mutually exclusive, in-so-far as species with otherwise uniform and cryptic pelages (consider the Eurasian badger *Meles meles*) announce their presence as soon as they raise their face masks and compromise their otherwise good bodily camouflage with this conspicuous headflag. We find no good association between facial masks and crypsis.

Do facial markings serve as an antipredator warning signal?

All masked species of medium sized carnivores are relatively ferocious and aggressive, and could potentially cause harm to a larger predator or competitor. When we compared several features of these species with midguild carnivores that do not have masks, we found that species with masks were primarily terrestrial and could potentially be caught in open habitat in which there are few if any refugia or places to escape (Table 1). Additionally, these species are relatively slow moving and not as agile or fast as many canids or felids. By contrast, we noted that unmasked midguild carnivores were able to utilize sites of refuge to effect an escape from a larger predator, e.g. otters/mink can escape into water, martens/mesofelids/civets can escape into trees, many mongoose species seek refuge in their burrow systems.

The masked midguild carnivore species, though predators themselves, all coexist with larger carnivores that could potentially kill and predate on them. Therefore,

warning or aposematic coloration could be advantageous if it served as a visual signal to deter further attack by larger predators. For warning coloration to be effective as a predator deterrent, the individual bearing the visual signal must be capable of defending itself and potentially harming an attacker. In many ways this warning coloration is analogous to the way that ungulates use pursuit-deterrent antipredator displays (Hasson 1991, Caro 1994) utilizing conspicuous color markings, such as the tail “flagging” seen in white-tailed deer (Caro et al. 1995). However, in midguild carnivores the message is “you don’t want to catch me”, rather than “you can’t catch me”.

The data presented in Table 1 show that each species with a facial mask coexists with one or more carnivores that are large enough to be a threat, but also close enough in size or fighting ability to be injured by the masked species. The data are consistent with the hypothesis that facial masks could be a visual signal or warning to any predator that further attack would be met with a counter attack that potentially could be harmful to the perpetrator. An additional factor that was likely a precursor to the facial mask serving as a warning was that most of these species possess anal scent glands and several of the members discharge noxious odors from these glands as a predator deterrent. Thus, discharging a noxious defensive spray that disables an opponent could have led to aposematic coloration as warning against this spray. In that most of the species with facial masks belong to families in which anal secretions are prominent, scent dissemination and corresponding aposematic coloration could have been a precursor to facial masks as warnings in themselves.

Testing the hypotheses: a model of the distribution of masks

Developing the hypotheses examined above we resolved upon 4 key variables with the potential to dictate whether a species (or group of related phylogenetically linked species) was likely to display aposematic facial markings.

The weight of the species was used as a predictive variable, categorized as (1) >100 kg; (2) 10–99 kg; (3) 1–9.9 kg; (4) <0.99 kg. Potential to escape from possible predators was considered. Species with the potential to escape predators (e.g. agility, arboreal or aquatic refugia) were categorized as (1); species vulnerable to predation were categorized as (2); species with no realistic predator (though consider the example of the spectacled bear, below) were categorized as (3). The ability of the species to put up a substantial fight (deterrent) toward a potential predator was also taken into account. Those with considerable fighting ability (e.g. large cats/bears) were categorized as (1); smaller

species that nevertheless display significant ferocity (/chemical defence) were categorized as (2); species with some ability to defend themselves were categorized as (3); relatively defenceless species were assigned (4). The extent to which species rely upon crypsis to hunt was also considered, with aposematic facial markings considered to compromise their hunting ability. Species needing very little crypsis (e.g. insectivores) were categorized as (1); species occasionally requiring crypsis (omnivores) were categorized as (2); species frequently requiring hunting crypsis were categorized as (3); species that rely heavily on crypsis to hunt ~the purely predatory species, were categorized as (4). "Masks" were categorized as (1) present; (2) absent as used as the response variable.

A Decorana analysis was performed to visualise the similarity between the taxa with regard to the four predictor variables. Figure. 2 (jittered score achieved automatically with SAS routine) plots each species according to its score on the first 2 axes derived from the ordination. The output shows that those species with masks are congregated in the upper right quadrant of the figure, determined by the axis scores for the predictive variables. GLMs for both axes 1 and 2 differ highly significantly between masked and unmasked species ($F_{1,238} = 80, P < 0.001$; $F_{1,238} = 40, P < 0.001$).

Despite phylogenetic linkage within masked genera (and within unmasked genera), limiting independence, the analysis revealed that within the evolutionary heritage of this group the factors of medium size, relative ferocity, exposure to predation and a reduction in the need for hunting crypsis were significant in militating for the evolution of aposematic facial markings. That "all"

skunks have masks does not detract from the observation that "skunks" have masks.

Predictions of the antipredator warning signal model

Our model predicts that terrestrial, relatively slow moving, midguild carnivores that do not regularly seek or have access to refugia and have evolved in the presence of larger, potentially harmful carnivores will possess contrastingly colored facial masks as aposematic warning where they are capable of a fierce and potentially damaging retaliation to attack. Notably, masks may confer several simultaneous advantages to a species, and thus underlying hypotheses should not be considered to be mutually exclusive. Of the 239 terrestrial carnivores in our sample (Macdonald 2001), the Felidae eliminate themselves as candidates on account of being swift predators that rely on crypsis to hunt, despite the appropriate size of many *Felis* sp.

The Ursidae, despite a tendency towards omnivory rather than predation, are all too large to be threatened by other predators (though see special reference to Andean bear, *Tremactos onatus*, below).

Amongst the Hyaenidae, the need for hunting crypsis overrides the potential for masks to be an evolutionary advantage in the presence of larger predators. They are also sufficiently swift to escape from larger guild competitors. Additionally, vocalisations play a significant role in hyena behaviour and warning calls at the approach of potential predators would obviate the requirement of warning coloration. Notably, the aardwolf, *Proteles cristatus*, specialising on termites and

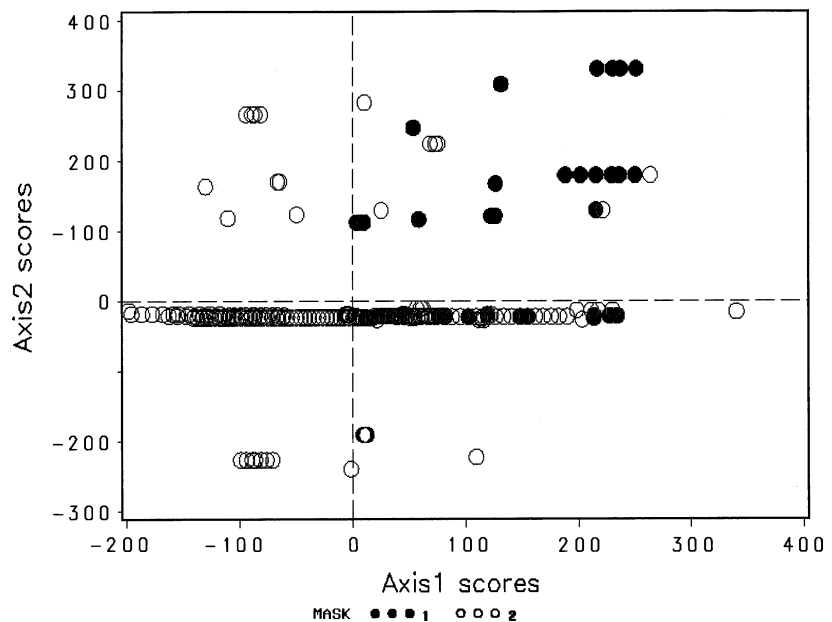


Fig. 2. A Decorana plot (jittered) of the distribution of species on the basis of size, escape potential, fighting ability and crypsis; polygon highlighting masked species.

weighing in at 8–10 kg, would be a candidate midguild carnivore for crypsis to develop. We speculate that the poorly developed jaws and teeth of the aardwolf probably do not provide it with sufficient defence against large east African felids to reinforce aposematic facial markings with genuine ferocity ~crypsis to hide from potential predators is probably more important.

In the majority, the Canidae are fast moving hunters that require crypsis for the successful pursuit of prey. Where canids are less predatory and more generalist, face masks have evolved (Table 1).

The Mustelidae include many members which either rely on crypsis for stalking prey, or crypsis to protect themselves from aerial predator to which they can mount little defence (weasels). Otters/mink can seek refuge in water bodies, while martens can find sanctuary from larger predators in trees. The remaining mustelids possess facial masks (Table 1).

The Mephitidae would all be vulnerable to attack by larger predators. Crypsis has little advantage to skunks as they consume a generalist diet. Instead, all species advertise their potent chemical defences with aposematic coloration and facial masks (Table 1).

The Procyonidae are generalist omnivores vulnerable to attack from larger predators when foraging on the ground, but able to defend themselves in these scenarios. Facial masks occur commonly in this family (Table 1).

The Viverridae and Herpestidae fall into the meso-carnivore size range vulnerable to attack from larger predators. Among these families, arboreal refugia and the need for camouflage while hunting prey militate against aposematic face masks in many species. Only members of the generalist feeding and terrestrial palm-civet subfamily (Paradoxurinae) possess face masks (Table 1).

Are midguild carnivores a threat to larger carnivores?

The midguild carnivores with facial masks appear to be formidable opponents to larger carnivores and present a danger at odds with the scaling of their predatory guild. These midguild carnivores are at some risk from their larger competitors (e.g. badgers, *Meles meles*, predated upon by wolves, *Canis lupus*, Liu and Jiang 2003) but any agonistic encounter is also a high risk for larger guild carnivores. The honey badger, or ratel, is especially ferocious and will even attack horses (*Equus caballus*), cattle and buffalo (*Syncerus caffer*) (Nowak 1999) and wolverines (*Gulo gulo*) have been reported to drive bears (*Ursus arctos*) and cougars (*Felis concolor*) from a kill (Cahalane 1958). American badgers will attack and drive off domestic dogs (*Canis familiaris*) (Cahalane 1958) and coyotes (*Canis latrans*) (M. Bekoff, pers. comm.) as will

raccoons (*Procyon lotor*) (Cahalane 1958). European badgers (*Meles meles*) are known for their ferocity if challenged and historically have been the foundation of a subculture of “badger baiting” in parts of Europe. Domestic dogs, specifically bred for fighting ability, are pitted against badgers in an arena with dogs frequently being maimed or killed by badgers in these contests (Neal 1990). Hog badgers, polecats, and various members of the Mustelidae are known for their “boldness and fearless courage to fight in self defence” to ward off attackers while spraying them with noxious discharge from scent glands (Prater 1971). Walker (1964) reports on incidences where domestic dogs were asphyxiated by the smell of the secretion from the teledu (*Mydaus javanensis*) and blinded in cases where the secretion was sprayed into the dog’s eyes. Similarly, the Palawan stink badger (*Mydaus marchei*) can also discharge its anal glands with great accuracy up to a distance of at least 1 m (Grimwood 1976). Members of the strikingly marked skunk family (Mephitidae) are particularly characterized by their ability to deter much larger predators with projectile anal gland secretions (Johnson 1921, Guilford 1990). Even considering smaller masked carnivores, these species still retain the capacity to injure or deter attacks from larger competitors from the tier of the guild immediately above them. For example, domesticated polecat-ferrets (*Mustela putorius furo*) are still listed as dangerous animals in the state of California by the Department of Fish and Game and cannot be kept as domestic pets despite their size relative to human handlers. Thus, overt aggression, threat of fighting, and spraying noxious discharge are traits characteristic of this group of midguild carnivores.

Does conspicuous coloration alert the prey of the midguild carnivore?

The midguild carnivores with masks tend not to hunt prey that is likely to observe them from a distance. However, facial markings, rather than full body markings do give the masked carnivores a degree of control over whom they display their warning coloration to; to deter predators/competitors if threatened, but not to attract attention in the first instance. Many of the masked midguild carnivores dig out subterranean prey (e.g. badgers), or chase prey underground (e.g. ferrets, polecats). Others are predominantly insectivorous or omnivorous (e.g. raccoons, coatis and ringtails, *Bassariscus astutus*). Interestingly, these species all hunt and forage with their noses to the ground such that their faces are not readily distinguishable from a distance. Small mammal prey (mice, voles) that are hunted in dense grassland habitats are small and unlikely to have the perspective to be visually alerted to a predators approach. Perhaps not coincidentally, midguild carni-

vores that do hunt prey by stealth-and-chase tend not to have these conspicuous colorations, e.g. ermine, martens and many foxes. Thus, midguild carnivores relying on crypticity to hunt prey may be mutually excluded from using aposematic markings as an antipredator warning.

Why don't all midguild carnivores have facial masks?

Not all of the midguild carnivores in these four families (Table 1) have facial masks. The two best correlates that emerged from our data are that closely related species that do not possess facial masks either have alternative means of escaping or avoiding predators or are predominantly predatory and would compromise their ability to approach their prey stealthily (Table 1). For instance, among the mustelids sea otters, river otters, and mink avoid terrestrial predators by being primarily aquatic and spending little time on land and thus are not vulnerable to larger terrestrial predators. Additionally, anal sacs in otters are absent or reduced considerably making scent a less potent weapon against larger predators (Ewer 1973). Marten occur in forest habitat, are arboreal and are usually close to trees that provide a readily available avenue for escape. Interestingly however, several species of marten as well as weasels possess contrasting colors on their chins and throats that would be visible in a frontal but not aerial confrontation. Fishers are also adept at climbing and considered amongst the best mustelid climbers (Cahalane 1958). Additionally, fishers seem to suffer little from predation by larger carnivores (Powell 1993 and pers. comm.). Among the procyonids, the unmasked kinkajou (*Potos flavus*) is almost entirely arboreal and does not overlap with other larger predators; by contrast to the masked and more cursorial raccoon and coati do have larger predators in their ranges. Among the civets, the few species that have masks appear to be more terrestrial, occur in open habitats, and have fewer refugia than closely related species without facial masks that are more arboreal and forest dwelling (Table 1; Nowak 1999, Macdonald 2001). Thus, these latter species should be able to avoid confrontation with larger predators by escaping to refugia. If escape routes were readily available and these individuals did not have to fight defensively against larger predators, selection may not have been strong enough to favor an aposematic warning coloration in these species. In contrast, 21 of 36 masked species in Table 1 occur in open habitats that do not provide escape refugia.

The remaining carnivores from these same families that are primarily terrestrial and do not have conspicuous facial masks are relatively small, weighing less than

1 kg, and thus occupy a different guild status and are therefore subject to different selection pressures. This size is probably below some minimal threshold that, even with warning coloration, would not be a threat to larger carnivores. Additionally, smaller carnivores such as weasels are typically killed and eaten by hawks and owls (Cahalane 1958). Thus a solid color, or lack of conspicuous markings, might be more suitable as camouflage to avoid detection. Also, with the smaller body size, individuals have access to more underground burrows and refugia than would larger carnivores. King (1989) suggested that the black-tipped tail in weasel species served to confuse predators helping them to escape. Only 8 of 36 species with masks weigh around 1 kg and the remaining 28 species weigh more than 2 kg and would be a relatively formidable opponent for larger carnivores. The smaller masked species appear to have relatively smaller predators/competitors (e.g. polecat and red foxes; ferrets and coyotes; and Patagonian weasel *Lyncodon patagonicus* and gray fox *Urocyon cinereoargenteus*) and thus even with their small size may be able to defend themselves against the only slightly larger predators. Additionally, these smaller masked midguild carnivores appear to have more well developed scent glands and produce stronger and more noxious odors than some of the other less conspicuously marked mustelids of this size. The larger masked carnivores seem to have larger predators (e.g. tigers, *Panthera tigris*, bears and wolves; Table 1) and thus relative size difference within guilds among sympatric carnivores may be an important feature favoring aposematic coloration.

The enigma of the giant panda

A few larger carnivores also possess conspicuous colour markings around the eyes such as the giant panda, *Ailuropoda melanoleuca*, and the Andean bear. Although these two species do not seem to fit our hypothesis in that they do not currently have larger predators, we surmise that sometime in their evolutionary history, this coloration had an aposematic effect. Did tigers or perhaps in prehistoric times, sabertooths, *Smilodon* sp., provide sufficient predation pressure to favor aposematic coloration in these species? Wolves historically have been predators on young pandas (D. Kleiman, pers. comm.). We do not know the ancestral relationships between these species and competitors or potential predators, but we suggest that selection pressures for coloration in pandas and Andean bears were similarly evolved in response to the presence of a larger predator in their local guild, as presented for the midguild carnivores.

A transition from noxious scent to warning coloration to face masks

Distinctive contrasting facial markings such as those described above may forewarn predators of the fighting ability of individuals, or they may be a form of mimicry mimicking the aposematic coloration of similar species in which conspicuous contrasting coloration is a warning of noxious odor. Several species of midguild carnivores such as skunks (all 10 species), stink badgers (2 species) and the zorilla (*Ictonyx striatus*) do not have facial masks per se but have distinctly colored black and white stripes or spots that serve as warning coloration. In these species, the aposematic color warning is reinforced by a noxious odorous spray that is a predator deterrent (Johnson 1921, Walker 1964, Grimwood 1976, Guilford 1990). In addition to face masks, some weasels such as the north African striped weasel (*Poecilictis libyca*) and its close relatives have conspicuous black and white skunk-like markings over their entire bodies and also eject a malodorous fluid that repels predators (Nowak 1999). Red pandas (*Ailurus fulgens*) have been observed giving off a strong odor from the anal gland under stress or excitement (Prater 1971). Civets, like skunks, produce a noxious odor from anal "stink glands" that repels predators. According to Prater (1971) the discharge is so acrid and nauseating that it temporarily blinds and frustrates an attacker allowing the civet to escape. Interestingly, palm civets (*Paradoxurus hermaphroditus*) living in northern areas of their range in China and Burma where they have many predators are boldly masked in black and white, whereas those living in the Adamans where there are scarcely any enemy carnivores have considerably less conspicuous facial markings (Prater 1971). Polecat species similarly are conspicuously colored and produce a noxious fluid discharged from anal glands when alarmed or attacked by larger carnivores. Under stress or excitement, polecats, like skunks and other members in this group, erect their hairs displaying even greater contrast between light and dark coloration. All mongooses have anal scent glands, but none have facial masks. However, only the striped-necked mongoose (*Herpestes vitticollis*) and the crab eating mongoose (*H. urva*) use their scent glands in defence (Prater 1971, Ewer 1973). Interestingly, these are the two most brightly and contrastingly colored species of mongoose possessing broad distinctive neck stripes and bright red coloring in *H. vitticollis* and badger-like gray and white markings in the crab eating mongoose. These two species are also larger (3 kg and 2 kg, respectively) than the other mongooses and would be more formidable foes to larger carnivores than would the smaller nonmasked species.

We propose that face masks in midguild carnivores are first an extension of the conspicuous warning coloration as seen in skunks, polecats, civets, and other species in

which an attack would result in a noxious spray of scent and second that further attack would be met with a relatively formidable counter attack by a relatively aggressive opponent. In that this group of midguild carnivores produces noxious odors and are probably quite unpalatable, a fore-warning against attack may be beneficial to both predator and potential prey. Larger predators that might attack these midguild carnivores also have an excellent sense of smell, which might make the scent even more opposing. The fact that some species with masks that are not known to have strong scent glands or spray a noxious scent, such as the raccoon, coati, raccoon dog, and bat-eared fox suggests that some feature other than a noxious spray may be sufficient to warn off predators. We suggest that in some species, the aggressive counter defence of midguild carnivores is sufficient in itself to select for aposematic colored face masks as a warning coloration.

Masks have a polyphyletic origin

Facial masks and other proposed aposematic pelage coloration in carnivores have a polyphyletic origin evolving independently in four Carnivore families and several times within a family (Table 1). In that these species in the different families have been subjected to the same ecological and behavioral forces, selection may have favored convergence and mimicking facial markings as antipredator aposematic warning signals. The four families of carnivores that represent species with facial masks, weasels (Mustelidae), raccoons (Procyonidae), foxes (Canidae), and civets (Viverridae) have a polyphyletic origin dating back to the Eocene (Macdonald 2001). The Vulpavines (Caniformia) which include the weasels, raccoons, and foxes, separated from the Viverines (Feliformia) in the early Eocene. The families within these two lineages separated from each other at varying times from the Oligocene to the early Miocene. Even within each of these families, and in some cases subfamilies, some species have conspicuous facial or body markings, whereas others do not, suggesting that color patterns have evolved independently in each family, and in some cases within genera (Table 1). We consider the polyphyletic evolution of masks to be an example of convergent evolution (Martin 1989), confined to terrestrial ecomorphs that do not hunt prey by stealth-and-chase, and do not climb trees, use burrow systems or dive into water to escape from larger predators. Those carnivore taxa that do not include masked representatives include only species that fall outside the niche in which masked midguild carnivores occur. Thus, it is behavioral ecology, rather than evolutionary ecology, which militates for the evolution of face masks. In contrast to Ortolani (1999) who proposed that many color patterns in carnivores are a response to environ-

mental or ecological pressures (e.g. camouflage), we conclude that masks in mammalian carnivores result from selection to warn and deter intraguild competitors and predators within a clearly defined niche.

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