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The evolution of anterior coloration in carnivorans

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Abstract

Some carnivorans have striking patches of fur on their faces (spots, bands, eye masks) and blazes on their chests that are primarily visible from a frontal view. We tested five hypotheses to explain the evolution of the complexity and contrast of these color patches. These were: signals of species identity to avoid hybridization, communication between conspecifics, signals used to warn of defensive anal secretions, signals of belligerence or pugnacity, and camouflage-related coloration used to break up the outline and facial features of the predator when approaching prey. Using phylogenetically controlled multifactorial analyses in six different families of carnivorans, examined separately, our analyses uncovered significant positive associations between measures of color pattern complexity and sociality across herpestid faces and canid chests, suggesting use in social communication. Mustelid facial color complexity was associated with ability to direct anal secretions accurately at predators, and facial markings were significantly or marginally associated with pugnacity

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in mustelids, viverrids, and herpestids. Facial complexity of viverrid and herpestid species was significantly or marginally related to a mammal-based diet. In ursids, facial contrast appeared less variable in species living in greater sympatry with other bears. Facial and chest coloration in Carnivora appears to have evolved under different selection pressures in different families.

Significance statement

The reasons that many carnivorans have colorful and memorable faces and chests are not vet understood. Here, we pit five different hypotheses against each other: species recognition, advertising either toxic anal defenses or pugnacity, recognizing group members, and trying to remain concealed when approaching mammalian prey. We find that measures of facial and chest complexity and contrast have evolved for different reasons depending on the carnivoran family. Anterior coloration appears to be involved with social communication in herpestids and canids; facial coloration is associated noxious secretions in mustelids, with pugnacity in mustelids, viverrids and herpestids; with reliance on a mammal-based diet in viverrids and herpestids; and with avoiding hybridization in bear species. There is no overriding evolutionary explanation for varied facial and chest pelage coloration across carnivorans.

Keywords Carnivores · Chests · Color complexity · Contrast · Faces

Introduction

To understand the evolutionary significance of external coloration in animals, we often focus on overall appearance because protective coloration, for example, will usually involve the whole animal being either cryptic, so as not to be detected, or conspicuous so as to signal to a predator or conspecific from a distance. Yet head coloration often differs from the rest of the body in many vertebrates, including reef fish, agamid lizards, marmosets, and parrots, as well as invertebrates such as paper wasps and caterpillars. In some of these species, coloration and patterns on parts of the head are known to function as signals to conspecifics, conveying information about individual identity, physiological state or species identity (Hill 2015; Tibbetts et al. 2017), or as signals to heterospecifics conveying information about species identity or defenses (Caro and Allen 2017). On the other hand, coloration patterns might break up the outline of the face to reduce the probability of the animal being recognized as a predator or prey (Cott 1940).

Certain orders of mammals have notably colorful facial and chest pelage patterns, particularly primates, carnivorans, and some artiodactyls (Caro 2013); however explicit tests of adaptive hypotheses to explain these patterns are scarce (Caro 2009). To summarize briefly what we know at present: platvrrhine neotropical primate (Santana et al. 2012), Old World catarrhine (Santana et al. 2013), and cercopithecine guenon (Allen et al. 2014) species all show greater facial color pattern complexity when living with a greater number of species belonging to the same genus or family. Whereas neotropical primates show greater facial color pattern complexity in species that live in smaller groups (Santana et al. 2012), catarrhines show greater facial complexity in more gregarious species (Santana et al. 2013). These independent effects suggest facial coloration serves as a species marker that may reduce risk of hybridization and possibly help in individual identification within social groups.

Dark-faced artiodactyls live in intermediate or large groups and are also pursued by coursing predators, suggesting that facial coloration may function in various forms of intra- and interspecific communication. Artiodactyls with white faces are diurnal, live in bushland or grassland habitats, and in intermediate-sized groups, so it is unclear whether their facial colors may be involved in signaling to conspecifics, aid in thermoregulation, or both (Stoner et al. 2003).

Some carnivoran species that are pugnacious or employ noxious anal secretions (e.g., mustelids and mephitids) have conspicuous facial coloration (Stankowich et al. 2011; Caro et al. 2017). Furthermore, carnivorans with facial stripes are middle sized, are dangerous to confront, and are more likely to use burrows or dens (Newman et al. 2005; Stankowich et al. 2011) where only their faces may be visible. Nonetheless, other carnivoran species have even more intricate and chromatic anterior coloration (see Fig. 1 for examples), and the complexity of such patterns on the chests and faces suggests that they could be used for purposes other than aposematism, especially since families like ursids do not use anal secretions for defense.

In this paper, we examine carnivoran anterior coloration using two measures: the number of different shades (pattern complexity), and the contrast among those shades, in six different families of carnivorans. Across this extensive sample (31 canids, 44 mustelids, 35 felids, 8 ursids, 19 viverrids, and 22 herpestids), we test several hypotheses that could explain the evolution of facial and chest coloration within the context of interactions with both conspecifics and heterospecifics. First, we test the hypothesis that anterior coloration is involved in conspecific recognition and maintaining reproductive isolation. We predict that the complexity of facial color patterns is associated with extent of species' sympatry at the family level (e.g., number of congeneric sypatric species), as previously reported in primates. Conspecific recognition could be a concern for carnivorans because free-living heterospecifics can interbreed (e.g., covotes Canis latrans and wolves Canis lupus in the northeast USA; Lehman et al. 1991). Second, we test whether anterior coloration varies in a way that is consistent with uses for intraspecific communication, in particular individual recognition. We predict that facial coloration is associated with species' sociality (e.g., Santana et al. 2012) such that species living in larger groups exhibit more complex facial coloration. Third, we reexamine whether anterior coloration is used as a warning to potential predators or competitors signaling extent of toxic anal defenses or of pugnacious behavior (see Ortolani and Caro 1996; Ortolani 1999). We predict that facial contrast and complexity is associated with noxious anal secretions, and then with pugnacity. Finally, we examine whether facial and chest coloration diversity in carnivorans is consistent with strategies for crypsis, in which facial coloration breaks up the outline of the carnivoran and makes it more difficult to recognize when approaching visually oriented prey. We predict that facial coloration is more complex and contrasting in those species that principally capture mammalian prey. We run analyses within carnivoran families as only closely related species present a danger as potential breeding partners.

Methods

Dependent variables

HW extracted up to 10 photographs of 164 terrestrial Carnivora species from books and reputable internet sites in which species identification was listed along with scientific name and, often, location (see supplementary material for full datset). Because photographs mined from the internet and books carry little information about camera sensors or illumination, we used several photographs of different individuals of each species. Calibrated photographs of museum specimens were not used because facial patches and patterns are distorted by the preparation process in museum skins, chest markings tend to

Fig. 1 Clockwise from top left: gray fox Urocyon cinereoargenteus, © Josh More / CC BY-NC-ND 2.0: ocelot Leopardus pardalis © Theodore Stankowich; sun bear Helarctos malayanus, © DSC5953 by Valerie / CC BY-NC-ND 2.0: slender-tailed meerkat Suricata suricatta © David Lewis / CC BY-NC-ND 2.0. Gray fox has a light gray forehead, red and white cheeks, black on lateral muzzle and white on anterior muzzle; chest patch is cream. Ocelot has black spots on a brown forehead, black-rimmed eyes surrounded by white, broad black stripes on cream cheeks, a dark brown and cream muzzle, and a cream chest with some black spots. Sun bear has a black face, eves rimmed with light brown, and a light brown muzzle; chest patch is creamy orange flecked with black. Meerkat has a light brown forehead, black-rimmed eyes, cream cheeks, and a light brown muzzle; ears are black



be obscured by ventral dissection, and pelts in older museum specimens undergo discoloration making them unsuitable (Davis et al. 2013). Each photograph was of an adult individual, and had enough resolution so that individual hairs and/or any banding on individual hairs were visible. Face shots were close-ups of the animal's face pointing toward the camera, although photographs with faces angled away from the camera were used as a last resort (amounting to <10% of all photographs). Photographs of deceased animals were used only very infrequently. All photographs had been taken during the day-time and had minimal glare, and photographs in which animals had wet, dirty, snowy, or windblown fur were avoided. Flickr and other non-scientific websites were used infrequently and only if the species was identifiable and not easily confused with others (see also Caro et al. 2017).

Each photograph was scored only once and only by HW. (In an earlier paper, a different scorer compiled a parallel dataset with fewer dependent variables but results of analyses were almost identical [Caro et al. 2017].) HW originally created 12 regions on the face (Fig. 2) loosely corresponding to how Santana et al. (2012) evaluated facial coloration in primates, as well as two regions on the chest (see Fig. 1a in Caro et al. 2017). In our sample, color coding of these regions was

based on the two forms of melanin present in mammalian hairs: eumelanin (black/brown pigment) and phaeomelanin (yellow/red pigment), and common combinations of the two. The color key for scoring facial regions consisted of seven



Fig. 2 Face of a coyote showing regions used to characterize facial coloration (see Caro et al. 2017)

categories: (A) no pigment (white), (B) no pigment banded with eumelanin black (silver), (C) eumelanin black, (D) agouti saturated with eumelanin (eumelanin and phaeomelanin banded hairs with predominantly eumelanin bands), (E) eumelanin brown, (F) agouti saturated with phaeomelanin (eumelanin and phaeomelanin banded hairs with predominantly phaeomelanin bands), and (G) phaeomelanin. All pigment categories (except no pigment white) had five gradations, each ranging from light or low pigmentation intensity (1) to dark or high pigmentation intensity (5) (Caro et al. 2017). Following scoring, color categories were rearranged by HW, TC, and TS, and forced into a common lightness-darkness scale of 1 (white) to 10 (black) (reading from left to right in Fig. 3).

Eleven regions of fur (excluding chins because they were often dirty) on photographs of carnivoran faces (median = 4 [interquartile range 2–6] photographs) and one region on the chest (median = 5 [interquartile range 2–8]) were compared to categories in A-G and assigned a best representative color (Fig. 2). Each facial region was scored independently of others. In cases where a region had 5% or more of an additional color, HW mentally divided that region into sections in order to estimate the percentage of each region for each color. (These percentage listings were especially prevalent in spotted and striped species.) Colors assigned to sections (or regions if 100% of one color) for each photo were converted into scores of 1 to 10 using the previously constructed color gradation scale (Fig. 3).

We constructed three facial scores as follows: (i) *Facial complexity* = the total number of different face shades across all sections; (ii) *Facial contrast* = the maximum difference in face shades based on the most extreme colors assigned to any section of any facial region, whether or not they were adjacent; and (iii) *Variability* = a measure of intraspecific variability

based on the standard error of facial contrast (see ii above) across photographs for each species for which we had four or more images of the face (note, species' facial variability was statistically unrelated to number of photographs examined in any of the six families). We expected reduced intraspecific variability in species under strong selection for a particular function.

We constructed two chest scores as follows: (iv) *Chest complexity* = the number of different chest shades across sections of the chest; and (v) *Chest contrast* = the maximum difference in chest shade based on the most extreme colors assigned to sections in the chest region. Data were scored blind because HW did not know of the facial and chest measures described above that were generated much later.

We only considered summer pelage for those species showing seasonal color change, and averaged scores from sexually dichromatic male and female African lions *Panthera leo*.

Independent variables

We examined canids, mustelids, ursids, felids, viverrids, and herpestids separately, dropping hyenids as they have only 4 species in the family. We used the number of sympatric species within the same family as the focal species to reflect pressures for species recognition. We assessed sympatry by measuring geographic range overlap of species' pairs taken from the IUCN website (www.iucnredlist.org). We conducted sympatry analyses irrespective of pairs' relative body weights, but additionally taking into account whether they differed by 25, 50, or 100% in weight. Results from these analyses were similar, and therefore only the first set is presented.



Fig. 3 Color key used for scoring anterior coloration, set on a 10 point light to dark shade scale shown from left to right (see Caro et al. 2017)

To examine the association between coloration and sociality, we employed a crude 4-point scale: 1 =solitary, 2 =pairs, 3 =groups reported as being of variable size, 4 =year-round stable groups, (taken from Caro et al. 2017). Defense categories (anal secretions) were taken from Stankowich et al. (2014): 0 = secretions not used in defense, 1 = secretions ooze out or they emit a foul smell when attacked, 2 = eject secretions in a stream (nondirected), and 3 = able to aim/direct the stream/spray of secretions at the predator. Pugnacity was scored as 0 or 1, with 1 representing reports of fierce or intimidating behavior; species recorded as unknown were assigned a liberal score of 1 (see Caro et al. 2017). We reran analyses assigning unknown species as 0, but results differed little and are not shown here.

The extent to which diet was composed of mammals was scored as 0 = known not eat to mammals at all; 0.1 = known to "mostly" eat non-mammals but it is unclear if mammals are ever taken; 0.2 = known to eat "small vertebrates" but no accounts of specifically taking mammals; 0.25 = known to "rarely" eat mammals; 0.5 = known to "sometimes" or "occasionally" eat mammals; 0.75 = regularly eat mammals but also eat members of at least two other taxa (e.g., birds, fish, insects); 1.0 = specializes in eating mammals but may take one other vertebrate group. Data were compiled from a variety of published sources (Kingdon 1977; Nowak 1999; Van Dyck and Strahan 2006; Francis 2008; Wilson and Mittermeier 2009; Hunter 2011; Myers et al. 2013).

All species' scores can be found in supplementary material.

Phylogenies

We downloaded a complete consensus phylogenetic tree of the carnivores from the 10KTrees website (Arnold et al. 2010). Some species names were changed to agree with those listed in Wilson and Reeder (2005). This consensus tree was then broken into the individual families above, and each family was analyzed separately.

Analyses

We conducted planned comparisons using targeted multifactorial phylogenetic comparative analyses to test individual hypotheses. Except where noted in the results, for each family we tested for the effects of the number of sympatric species within the same family, sociality, anal spraying ability, pugnacity, and mammalian diet. All of these predictor variables were tested together within the same regression models, and on each of the five coloration measures described above. We ran phylogenetic generalized least squares (PGLS) regressions using the "caper" package (Orme et al. 2012) in R (R Development Core Team 2008). Our rationale was that each model tested the effect of social and ecological variables on a different coloration feature, and thus a different phenomenon, and also that different hypotheses may apply differently across families. Since these are all planned comparisons, we did not apply *p* value corrections. For each model, lambda (λ which represents the phylogenetic signal) was computed using maximum likelihood methods. We report the N, degrees of freedom, λ , t-statistics, and *p* values with 0.1 representing marginal significance. Some factors could not be tested due to limited or lack of variation in that factor among the species sampled from the family (e.g., ursids all lack anal spray abilities and are solitary).

Results

Canids

Despite some canids having quite diverse facial features, we did not find a significant positive association between any measure of facial or chest coloration and any independent variable, save one: species with more complex shades on their chest were more gregarious (Chest complexity with Sociality; N = 31 species, df = 5, 25, $\lambda = 0$; t = 2.214, p = 0.036; Table S1).

Mustelids

We found significant positive associations between both the number and contrast of facial shades and ability to direct anal spray in defense (Facial complexity and Facial contrast with Anal spray N = 44, df = 5, 38, $\lambda = 0$; t = 2.286, p = 0.028; $\lambda = 0.682$, t = 2.520, p = 0.016, respectively). There was less variability in facial contrast in pugnacious species (at least marginally) and in those relying more on a mammal-based diet (Variability with Pugnacity and with Mammal diet N = 21, df = 5, 15, $\lambda = 0$, t = -1.895, p = 0.078; t = -2.625, p = 0.019, respectively; Table S2).

Felids

There were no significant positive associations between facial or chest complexity measures and any independent variable. Felids do not use anal secretions for defense (Table S3).

Ursids

There were no significant positive associations between shade measures and any independent variable in bears, except that there was less intraspecific variability in facial contrast in species whose geographic ranges overlapped with a greater number of ursid species (N=8, df=3, 4; $\lambda=0$; t=-3.549; p=0.024). Note all bears are solitary and none use anal secretions defensively, so these variables had to be dropped (Table S4).

Viverrids

There were few significant positive associations between facial or chest complexity measures and independent variables, except that species whose faces had greater contrast were more pugnacious (Facial contrast with Pugnacity; N = 19, df = 5, 13; $\lambda = 1.000$; t = 2.348; p = 0.035); and facial complexity was marginally associated with reliance on mammals in their diet (Facial complexity with Mammal diet N = 19, df = 5, 13; $\lambda = 1.000$; t = 1.976; p = 0.070; Table S5).

Herpestids

We found associations between facial pelage and measures of both sociality and pugnacity in this family. The number of different facial patches and contrast between facial patches were both significantly or marginally linked to increasing sociality across species (Facial complexity and Facial contrast with Sociality; N=22, df=5, 16, $\lambda=0$; t=1.956, p=0.068; t=2.682, p=0.016 respectively) and to pugnacious behavior (Facial complexity and Facial contrast with Pugnacity; N=22, df=5, 16, $\lambda=0$; t=2.553, p=0.021; t=1.868, p=0.080, respectively). There was also a significant positive association between facial complexity and a mammal-based diet (Facial complexity with Mammal diet; N=22, df=5, 16, $\lambda=0$; t=2.243, p=0.039; Table S6).

Discussion

This study examined two aspects of anterior coloration, namely shade complexity and shade contrast; lightness/darkness was chosen because most mammals are dichromats. Specific patches of color, or their shape, could convey different information about individual identity or health that we did not explore here. Our findings support an association between facial and chest shading and sociality at least in some carnivoran families. Specifically, facial shade pattern complexity and contrast were significantly or marginally associated with group living in herpestids, and chest shade pattern complexity was associated with group living in canids. This suggests that coloration cues on these anterior parts of the body could be used in conveying information (perhaps about individual identity or physiological state) to conspecifics with whom individuals associate regularly. Ortolani and Caro (1996) found a marginal association between white throats and sociality in viverrids, but sample size was small.

Our results mirror those in catarrhine primates, in which more gregarious species have more complex facial color patterns (Santana et al. 2013; but see Santana et al.2012 for a counterexample). These results raise the possibility that some carnivoran species may rely on visual means to recognize members of their own and other groups. This is perhaps surprising given they are dichromats, but notable given that olfaction is normally assumed to be paramount in intraspecific communication in this taxon (Gorman and Trowbridge 1989). Our results raise the possibility that olfaction and vision are used in potentially complex ways in individual recognition. Consistent with a potential role of coloration in social recognition, felids and ursids, which are the more solitary families, do not exhibit significant associations between anterior shading and sociality. There is insufficient variation in ursids to test for this relationship.

We were not surprised to find an association between an ability to spray noxious anal secretions and facial color pattern complexity and contrast in mustelids, which are mid-sized carnivorans. In fact, despite using very different methodologies, our findings are consistent with those of Newman et al. (2005), who showed that mid-sized carnivorans with facial stripes tend to be ferocious or possess anal secretions (indicative of aposematism; see also Stankowich et al. 2014). Moreover, species with facial stripes tend to use burrows or dens and their facial livery may deter attackers from entering their refuge (Stankowich et al. 2011).

Facial markings were also significantly or marginally associated with pugnacity in mustelids, viverrids, and herpestids. Intraspecific variability in contrast was marginally reduced in more pugnacious mustelid species, whereas viverrids and herpestids with more contrasting faces were significantly or marginally more belligerent, and more pugnacious herpestids had more complex facial patterns. Measures of pugnacity are extremely difficult to assess from the literature, we could only score it dichotomously, and are leery of this measure. Nonetheless, our results highlight that facial complexity might signal something about ferocity in these three carnivoran families (see also Newman et al. 2005). In separate, earlier analyses across the whole carnivoran order, contrasting ear markings were associated with pugnacity (Caro et al. 2017).

Facial shade pattern complexity in viverrids and herpestids was related to the extent to which mammals featured in these carnivores' diets. This result is consistent with a disruptive coloration function if mammalian prey principally uses vision to detect approaching predators: here, the pattern could serve to break up the predator's facial outline and features. Other families showed no such association although this would be unlikely in canids that spend little time stalking, or in bears that rely largely on plant foods; but is surprising not to find it in felids although their high reliance on mammalian prey may make it difficult to detect an association. Spotted and uniformly colored felids probably rely on background matching to avoid being detected by prey (Ortolani and Caro 1996; Allen et al. 2010).

We found that ursids showed less intraspecific variability in facial contrast in species that live in greater degree of sympatry with other ursids. There is considerable range overlap among the eight species of bears. The brown bear *Ursus arctos* has a

vast range across most of North America and Asia, overlapping extensively with the polar bear Ursus maritimus and the American black bear Ursus americanus, which overlap with each other in parts of Canada. The Asiatic black bear Ursus thibetanus overlaps with the range of the brown bear, giant panda Ailuropoda melanoleuca, sloth bear Melursus ursinus, and Malayan sun bear Helarctos malayanus, and the latter two species overlap in Bangladesh. Only the Andean bear Tremarctos ornatus is allopatric with all other members of the family. All bear species are of approximately similar body size, and four are within same genus, Ursus; moreover, freeliving grizzly bears Ursus arctos horribilis and polar bears Ursus maritimus can interbreed in Canada (Kelly et al. 2010). Due to their extensive range overlap and size similarities, features that enable species recognition to avoid hybridization may be favored, including distinct facial coloration.

There were no associations between facial shading and degree of sympatry in other carnivoran families. Perhaps dichromatic vision in carnivorans demotes differential shadiness of faces as a reliable tool for species recognition, compared to most Old World apes and monkeys and some New World female primates that have trichromatic vision (Osorio and Vorobyev 1996). Additionally, carnivorans are mostly nocturnal and may rely less on vision than primates that are almost entirely diurnal. Yet another possibility is that carnivorans are often territorial and asocial so that close up visual encounters are more infrequent than in primates.

In conclusion, we find preliminary evidence that diversity in facial and chest coloration in carnivorans is related to several different variables. Depending on the family, these relate to intraspecific communication, aposematism, approaching prey undetected, and reducing hybridization risk. These findings, though tentative, suggest that it is too simplistic to argue that colorful anterior areas of carnivorans' bodies serve only one function. Rather, different aspects of coloration (number of shades, contrast between shades and intraspecific variability) have apparently been shaped by multiple evolutionary forces, and these seem to vary across families, pointing to the danger of assuming that similar markings serve similar functions even within a single taxonomic order.

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Compliance with ethical standards

Ethical statement All sources of data were from the literature or the web and did not involve ethical approval. There was no funding for this project.

Conflict of interest The authors declare that they have no conflict of interest.

Data availability All data generated or analyzed during this study are included in the supplementary information files.

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