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ORIGINAL ARTICLE

Black-and-white pelage as visually protective coloration in colobus monkeys

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Abstract

Conspicuous coloration is often seen as the evolutionary consequence of either sexual selection or warning predators visually about prey defences, although not all conspicuous species fit this paradigm. Exceptions include several species of colobus monkeys whose black-and-white coloration, characteristic of larger colobines, has never been explained. Here, using photographs of black-and-white colobus (*Colobus vellerosus*) taken in the wild, quantitative image analysis, and vision modelling (acuity-corrected feline, chimpanzee, and raptor vision), we provide evidence that their coloration provides distance-dependent camouflage in natural forest environments. At all viewing distances, black-and-white colobus monkeys blend into their environment because of their high chromatic overlap with the background when viewed by ecologically relevant predator vision models which have low visual acuities. Additionally, for chimpanzee and felid vision, there was evidence of edge disruption at longer viewing distances. Our comparative analyses of different species of colobines do not support an association between black-and-white coloration and larger body mass or group size, but this may simply be due to the limited number of species within the family. We reason that black-and-white colobines gain visually protective coloration through background matching against felids, and also benefit through disruptive coloration against felids and chimpanzees but rely on these protective coloration mechanisms less against raptors.

Significance statement

Conspicuous black-and-white coloration in colobus monkeys has long eluded an evolutionary explanation. Our research, employing photographs of colobus monkeys, image analysis, and vision modelling, unveils a novel approach to this coloration. We show that in their natural forest habitats, black-and-white colobus monkeys employ distance-dependent camouflage against ecologically relevant predators with low visual acuity, blending in with the background at increasing viewing distances. In summary, the evolution of black-and-white colobus coloration appears to be related to background matching against felids, with added benefits of disruptive camouflage against felids and chimpanzees, less so to raptors, offering fresh insights into the complex interplay of coloration and survival strategies in mammals.

Keywords Colobus vellerosus · Background matching · Camouflage · Disruptive coloration · Primates · Vision model

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Introduction

Conspicuous coloration in animals is commonly assumed to function in visual signalling and communication (e.g., Cott 1940). Vertebrate examples include toucans, parrotfish, poison dart frogs, and coral snakes evolved to be flamboyant as a result of sexual selection (i.e., interspecific signalling) or aposematism (i.e., signalling unprofitability through their coloration), yet mammals rarely feature in such a list of gaudy species. Rather, mammals are renowned for being dowdy, dominated numerically by bats and rodents that are grey or brown to blend in with their background (Caro and Koneru 2021). Mammalian exceptions to this generalization are not particularly colourful, aside from some primate species (e.g., Winters et al. 2020; Bell et al. 2021; Caro et al. 2021); instead, these exceptions often have sharply defined achromatic black-and-white patches of pelage juxtaposed against each other. Examples include harp seals (*Pagophilus groenlandicus*) and ribbon seals (*Histriophoca fasciata*) at sea, terrestrial Malayan tapirs (*Tapirus indicus*) and giant pandas (*Ailuropoda melanoleuca*), and arboreal indris (*Indri indri*) and black-and-white ruffed lemurs (*Varecia variegata*). However, at present, we have only a rudimentary understanding of why these striking black-and-white appearances evolved and there appears to be no unitary explanation for contrasting coloration in mammals (Caro 2009, 2013).

Current understanding of conspicuous pelage coloration in mammals can be summarized as follows. Evidently, some black-and-white mammals are aposematic, the most obvious examples being the skunks (Memphitidae), which advertise unpleasant anal secretions using striking black-and-white stripes or blocks of pelage (Stankowich et al. 2011); crested rats (*Lophiomys imhausi*) are another example (Kingdon et al. 2012). Additionally, comparative evidence suggests that larger species of primates may use irregular blocks of black-and-white pelage to visually advertise potential difficulty in handling prey of large body size (Howell et al. 2021), another form of defence (Wallace 1867). Other black-and-white mammals are cryptic, such as giant pandas (*Ailuropoda melanoleuca*), which match their background at medium distances from an observer and additionally employ disruptive coloration to break up their outline at greater distances (Caro et al. 2017; Nokelainen et al. 2021). Yet other mammals utilize colour patterns to prevent parasite attack: the striped pelage of zebras (*Equus* spp.) thwarts attempts by biting flies to land on them (Caro 2016; How et al. 2020).

Disparate findings and different ecological contexts make it difficult to generalize to other black-and-white species, and proposed explanations ascribe different patterns of black-and-white coloration on the bodies of mammals to different functions involving sexual selection, lures, warning colours, badges of status, and disruptive coloration (Caro 2009). Thus, the function of coloration in species such as orcas (*Orcinus orca*), Malayan tapirs (*Tapirus indicus*), or black-and-white colobines must be studied afresh. From a general standpoint, randomly distributed patches might aid in camouflage as in spotted skunks (*Spilogale putorius*) (Caro et al. 2013), whereas more consistent patches might be better for standing out for visual signalling as seen in striped skunks (*Mephitis mephitis*) (Walker et al. 2023). The functionality of coloration may, however, be difficult to pin-point as its purpose interacts with multiple factors such as visual background, animal size, and lighting conditions. Furthermore, and non-exclusively, colours may serve non-visual functions (e.g., aid thermoregulation, structural strength of pigmentation or be linked to antimicrobial properties).

Contrasting pelage coloration is particularly curious in black-and-white colobus monkeys, a genus of catarrhine which lives in Eastern, Central, and West Africa (Wikberg et al. 2022). One species in the genus *Colobus* has black pelage (*C. satanas*), while the other four species are black with large areas of white fur superimposed on them: *C. angolensis*, *C. guereza*, *C. polykomos*, and *C. vellerosus* (Wikberg et al. 2022), the last of which we use here as an exemplar. *C. vellerosus* has a white tail, white patches on its thighs, and a white ruff that surrounds the facial region (Saj and Sicotte 2013). Each of the other three species has white fur around their facial region or prominent white tufts on the sides of their face that may droop below the cheeks. *Colobus guereza* has a "U" shape of long white fur that runs along the sides of their body, while *C. angolensis* and *C. polykomos* have long white shoulder manes. In some species, the distal part of the tail has a large white tuft; in others, including *C. vellerosus*, the proximal half of the tail is also bright white. Generally, these species are arboreal; inhabit dense forests; eat mostly leaves, fruits, and seeds; and live in unimale-multifemale or multimale-multifemale groups that in some species coalesce to form multilevel societies (Wikberg et al. 2022).

We explored three evolutionary predictions to explain black-and-white coloration in colobine monkeys: background matching, disruptive coloration, and aposematism. We applied an established image analysis protocol (e.g., Troscianko and Stevens 2015; van den Berg et al. 2020; Nokelainen et al. 2021) to a series of photographs of black-and-white colobus taken in the wild in Ghana to model how they would be seen by three vision models of documented predators: leopards (*Panthera pardus*), chimpanzees (*Pan trogolodytes*), and raptors such as martial eagles (*Polemaetus bellicosus*). First, to determine whether black-and-white colobus are cryptic, we quantified the background matching. We suspected that the black areas of fur might blend in

with the dark background of the upper canopy when viewed from below, whereas white patches of fur might blend in with bright patches of light shining through the canopy. Such "differential blending" (Cott 1940) has been shown to operate in the giant panda seen in its natural habitat (Nokelainen et al. 2021). Second, we tested the extent to which these markings break up the body's outline, making it plausibly more difficult to recognize (i.e., disruptive coloration; Cott 1940). We hypothesized that areas of black-and-white fur juxtaposed against each other, the boundaries of which are orthogonal to the animal's true outline, break up the body's outline. Such 'disruptive coloration' has been shown to operate in other black-and-white mammals, giant pandas, when viewed at a distance by natural predators (Nokelainen et al. 2021). Third, to investigate an alternative hypothesis for their appearance, warning coloration, we compared body sizes and group sizes of black-and-white colobus monkeys to other members of closely related genera within the family (Fig. 1): the red colobus (*Pilicolobus*) and the olive colobus (*Procolobus*). We assumed that if black-and-white colobus used their coloration to advertise their ability to defend themselves using large body size, there would be positive associations between coloration and body size as found across primates (Howell et al. 2021), and group size as primates can mount an effective defence against some predators when they attack a predator as a group (see Caro 2005 for a review).

Methods

Image collection

In total, 549 images of white-thighed colobus monkeys (*C. vellerosus*) in natural forest settings were collected opportunistically, out of which 84 were used in further analysis (see below). It was not possible to record data blind because our study involved focal animals in the field. Upon encountering a colobus monkey in the forest, a photograph was taken in RAW format of the monkey and the surrounding habitat. Photographs were collected at the Boabeng-Fiema site in Ghana by ECW and FAC in 2008, 2009, and 2012, using a Nikon D80 or a Canon EOS 40D camera. We selected images which were of good quality, in focus, contained a single individual and in which the monkey was not overly obscured by the foreground (i.e., no more, but often less, than approximately one fifth of an animal was allowed to have branches or twigs in the foreground, for practical reasons, as they live in the canopy).

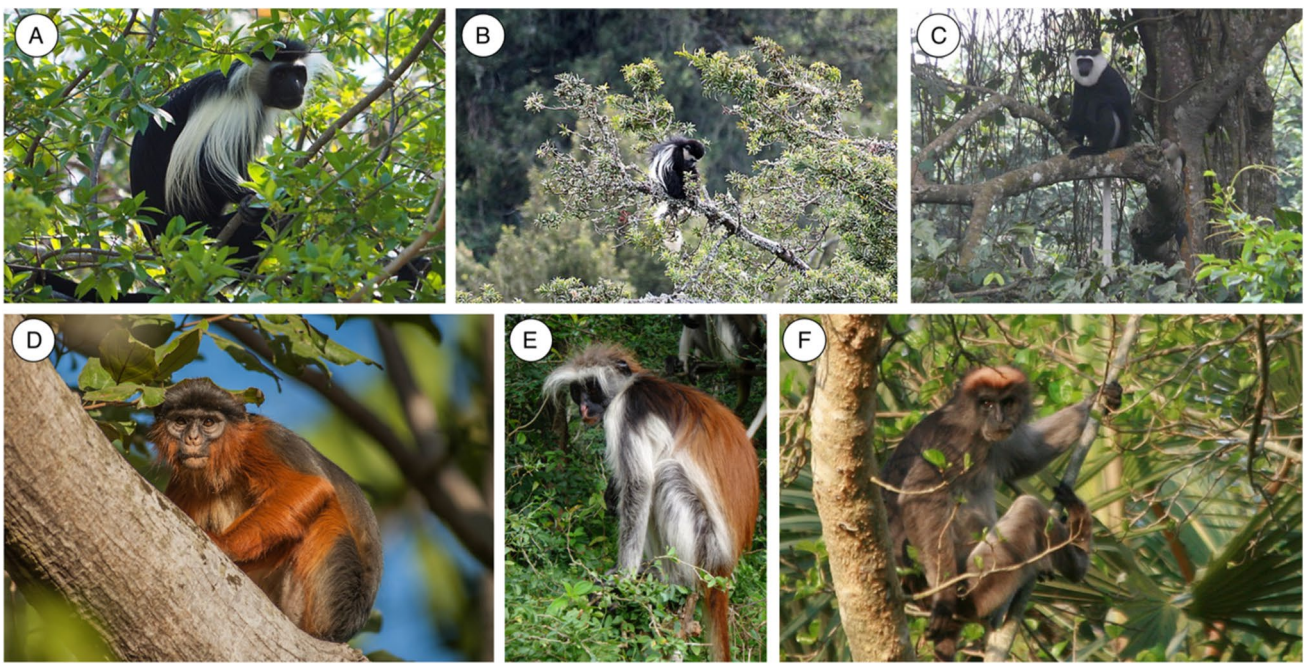

Fig. 1 Examples of primate species investigated in this study. The visual modelling exclusively focused on *Colobus vellerosus* (C), for which the most consistent photographic data was available. Phylogenetic comparisons were based on 11 species. Depicted here are three species black-and-white colobus: *C. angolensis* (**A**), *C. guereza* (**B**), *C. vellerosus* (**C**); and three red colobuses: *P. badius* (**D**), *P. kirkii* (**E**), and *P. ruformitratus* (**F**). All images are from Wikimedia Commons, are not normalised or scaled, and are reprinted under a CC BY 4.0 Attribution 4.0 international licence

Image processing

All images were processed using a common pipeline for animal coloration research (Stevens et al. 2007; Troscianko and Stevens 2015), employing a combination of the MICA toolbox (Troscianko and Stevens 2015; van den Berg et al. 2020) in ImageJ (Schneider et al. 2012), the pavo package (Maia et al. 2013, 2019) in R (R Core Team 2022), and custom-written MATLAB and R code (Winters 2023).

Colobus monkeys live high in the forest canopy, and images were necessarily collected without colour standards. There is no way to include Lambertian standards — the ideal method of calibrating such images — in true wildlife photography: our method followed here, however, allows us to standardize lighting across a visual scene and ask some basic questions about animal appearance. To overcome the lack of photographic standards, we took advantage of a previously used pragmatic approach (Nokelainen et al. 2021) to calibrate images based on the animals themselves. To account for differences in illumination, we measured black-and-white regions of the pelage and set these to 5% and 55% reflectance, respectively, based on measurements from a *C. guereza* pelt (National Museum of Natural History specimen number 163122) photographed alongside an X-Rite ColorChecker Passport 2 colour standard and normalized using the grayscale patches of the standard. The largest patch of white and black hair, clean and well-illuminated, was selected to measure the hair colour. To standardize monkey images for size, we measured the trunk length of the colobus monkey (i.e., the linear distance from the top of the head to the base of the tail) and used this "monkey length" as the unit for all subsequent measurements. The average *C. vellerosus* trunk size is 64 cm (Rowe and Myers 2016). As our image metrics compare colobus and background regions within the same image, our results should be robust to common image calibration procedures.

For each image, we manually selected regions of interest (ROIs) denoting the monkey and background. More specifically, we marked three ROIs: the visible monkey region, the whole monkey region (i.e., including the whole contour even if partially blocked by foliage), and the background. The visible monkey ROIs were made by combining all visible regions of the monkey body; this only included opaque hair, with any transparent hair on the edge of the individual not included. The whole monkey ROI was an approximate outline of the individual, resulting in a ROI that includes the visible monkey as well as some foreground foliage (i.e., including obscured body parts). For the background, the area surrounding the colobus monkey was selected, excluding anything in the immediate foreground or anthropogenic objects. The whole monkey region was then cut out of this background, leaving only the surrounding area.

Vision modelling

We used visual models to model perception by three predator visual systems: felids, chimpanzees (*Pan troglodytes*), and raptors. These three systems represent the black-and-white colobus monkeys' major predators in the wild (Fashing 2022; Wikberg et al. 2022).

We developed a cone catch model for each visual system based on camera and visual system data. The spectral sensitivities of the Nikon D80 were obtained from the MICA toolbox (Troscianko and Stevens 2015); raw sensitivities of the Canon EOS 40D were obtained from an online repository (Butcher 2020), interpolated from 400 to 700 nm, smoothed using a LOESS span of 0.05, and normalized to sum to one. Spectral sensitivity curves for each photoreceptor of the predator visual systems were generated using a rhodopsin template (Govardovskii et al. 2000) and peak cone sensitivities (λ_{max}), adjusted based on photoreceptor oil droplet properties (where relevant), scaled by the specular transmission of light through the ocular media, and normalized to sum to one. The dichromatic felid visual system was modelled on the domestic cat (*Felis catus*; λ_{max} = 454,561 (Loop et al. 1987); ocular media transmission from Douglas and Jeffery (2014)), with luminance perception based on the long-wavelength cone (Osorio and Vorobyev 2005). We modelled the trichromatic chimpanzee visual system (λ_{max} = 430, 535, 562 (Surridge et al. 2003); ocular media transmission from Douglas and Jeffery (2014)), with luminance perception based on the average of the medium- and long-wavelength cones (Osorio and Vorobyev 2005). Raptors are tetrachromats, but here we model only their "visible light" perception (long-, medium-, and short-wavelength cones), because our images do not include an ultraviolet channel. Both forest scenes (Willink et al. 2013) and primate pelage (Winters et al. 2014) reflect minimal ultraviolet light, so this omission is unlikely to influence our results. We modelled raptor vision based on a combination of common buzzard (*Buteo buteo*) and general avian visual system information (λ_{max} = 449, 504, 567 (Ödeen and Håstad 2003; Hart and Vorobyev 2005; Lind et al. 2013; Mitkus et al. 2018); oil droplet type = C, Y, R, λ_{cut} = 437, 509, 566 (Hart and Vorobyev 2005; Lind et al. 2013; Mitkus et al. 2018); ocular media transmission from (Lind et al. 2013)), with luminance perception based on double-cones (λ_{max} = 567; oil droplet type P, λ_{cut} = 460 (Hunt et al. 2009; Mitkus et al. 2018)). All images were modelled under a standard daylight (D65) illumination.

To account for the spatial acuity of each visual system, we used Fourier bandpass filtering to remove image information that would be imperceptible at a given viewing distance (Caves et al. 2018) based on the minimum resolvable angle (MRA) of each visual system (cat MRA = 1/10 (Wässle 1971); chimpanzee MRA = 1/64 (Spence 1934);

raptor (based on the wedge-tailed eagle *Aquila audax*) MRA = 1/140 (Reymond 1985)). Each image was modelled at 20, 100, 200, and 400 colobus lengths away (approximately 13, 64, 128, 256 m) for each visual system to gain insight on metrics as a function of distance. We chose a wide range of distances because the detection distance likely differs between terrestrial and aerial predators and depends on the forest strata and habitat type the colobus monkeys are in. The colobus monkeys use different forest strata (ranging from ground level to emergent trees at over 40 m height) and habitat types (primary forest, secondary forest, farmland, built-up areas, and roads) (Wikberg et al. 2022). While colobus monkeys at the top of emergent trees are likely visible to aerial predators at long distances, they may only be detectable at short distances in the dense understory. Thus, these distances were chosen to support visual modelling purposes, while keeping in mind ecologically relevant distances under natural conditions: in dense forest, environment visibility could be less, but modelling distance farther away gives us a better understanding of how crypsis is modulated by distance. Resulting images were scaled to three pixels per MRA unless this would increase the resolution of the image.

We then generated clustered images in which pixels perceived as a continuous colour are grouped together. Clustered images were generated using the quantitative colour and pattern analysis framework (van den Berg et al. 2020), which uses the receptor-noise-limited (RNL) model (Vorobyev and Osorio 1998; Vorobyev et al. 2001) to determine discrimination thresholds. This approach is based on Weber fractions that quantify receptor noise. We calculated chromatic Weber fractions (w) for each visual system based on receptor specific noise (v) and cone ratios (n) using the formula $w = v/\mathrm{sqrt}(n)$, using $v = 0.05$ for the most numerous cone and cone ratios (normalized to the most numerous cone) calculated based on receptor densities (sw:mw:lw; cat: 1:6 (Loop et al. 1987; Linberg et al. 2001); chimpanzee: 1:16:16 (Knoblauch et al. 2006), raptor: 1:2:2 (Lind et al. 2013). Luminance Weber fractions were obtained from the literature for each visual system (cat $w = 0.07$ (Chiao et al. 2000); chimpanzee $w = 0.08$ (Osorio and Vorobyev 1996; Osorio et al. 2004); raptor $w = 0.1$ (Lind et al. 2013; Potier et al. 2018)). We ran RNL ranked filtering, which smooths images while retaining edges, and RNL clustering, which clusters filtered images, using recommended parameter values (RNL rank filtering: iterations = 5, falloff = 3; RNL clustering: loops = 20, radius multiplier = 2, compare = 6, stop = 1, record = 20 (van den Berg et al. 2020)). For clustering, we set the chromatic and luminance just noticeable difference threshold to one (i.e., the discrimination threshold for the visual system) and the minimum cluster size to the number of pixels per MRA of the image (i.e., the minimum resolvable region for the visual system).

Image analysis

To quantify the contrast between the colobus monkey and the background, we calculated the proportion of the colobus monkey that overlapped chromatically with the background in the clustered images. For each cluster in the whole colobus monkey ROI, we determined whether that cluster also existed in the background ROI, yielding a set of clusters "inside" and "outside" the background. We then calculated the number of colobus pixels inside and outside the background based on their assigned cluster, yielding a pixel ratio (number of colobus pixels inside the background: number of colobus pixels outside the background), which we used as our measurement of background matching. To account for additional potential covariates, for each image, we also measured the proportion of the image that included the colobus monkey ("size in frame" = number of pixels in the whole colobus monkey ROI/number of pixels in the background ROI) and the proportion of the colobus monkey obscured by foliage ("occlusion" = (number of pixels in the visible colobus ROI − number of pixels in the whole colobus ROI)/number of pixels in the whole colobus ROI).

To quantify disruptive coloration, we used a subset of randomly chosen fifteen monkey images, which were processed through three vision models and four distances (i.e., $15 \times 3 \times 4 = 180$ images were analysed for edge disruption). We used Gabor filtering of achromatic (i.e., probing only through the luminance channel) edge disruption to quantify the ratio of false edges that run orthogonal to an animal's outline. We quantified whether edge disruption operates as a function of distance and hypothesized that edge disruption should operate more effectively on animals further away because as the distance between predator and prey increases, the latter's outline will become less detectable than the disruptive markings. At the limit of object detection both disruptive markings and the animal's outline should become undetectable. The distance was modelled as relative body lengths (i.e., the colobus body length was set as 1). We modelled the distance to target using the visual acuity tool in the MICA toolbox with sequence increments for longer distances. A GabRat Sigma value of 3 was used. We reasoned that maximal edge disruption should be close to 50%, because beyond this, the "false edges" become predominant (i.e., leading to the same "issue" as having an outline).

Comparative data

To conduct phylogenetic comparative analyses, the taxonomy of African colobines (genera *Colobus*, *Piliocolobus*, and *Procolobus*) was first matched to the 12 species of colobus monkeys included in the species-level phylogeny of mammals used in Upham et al. 2019. Altogether in phylogenetic comparisons, we had 11 species: five from the

black and white colobus complex (*C. satanas, C. angolensis, C. guereza, C. polykomos,* and *C. vellerosus*), five from the red colobus complex (*P. badius, P. kirkii, P. pennant, P. preussi, P. ruformitratus*), and the olive colobus (*P. verus*). Udzungwa red colobus was excluded from comparative analysis owing to unavailable data on adult body mass for that species. Photographs of each species collected from various online databases, including Nature Picture Library, iNaturalist, and Global Biodiversity Information Facility (GBIF), were then used to determine which species possessed only black-and-white coloration. Data on species' average social group sizes were collected from PanTHERIA (Jones et al. 2009), and average adult body mass values were collected from volume 3 of Handbook of the Mammals of the World (HMOW) (Mittermeier et al. 2013).

Statistical analysis

We analysed the degree of colobus background matching using beta-binomial generalized linear mixed models (GLMMs), implemented using the "glmmTMB" package v. 1.1.4 (Brooks et al. 2017) in R v. 4.2.1 (R Core Team 2022). We set the number of colobus pixels that did (or did not) occur in the background as a binomial outcome variable in which pixels have varying but unobserved underlying probability of being inside or outside the selection. We included visual system (felid, chimpanzee, raptor), distance (20, 100, 200, 400 colobus lengths), size in frame (the proportion of the image area that included the colobus monkey), and occlusion (the proportion of the colobus monkey obscured by foliage) as fixed effects, and visual system by distance interaction. Image was included as a random effect to account for repeated measurements of the same visual scene. The model was fit to a beta-binomial family distribution, and numerical predictor variables were scaled before inclusion. Model checks were run using the "DHARMa" R package v. 0.1.6 (Hartig 2022). We used likelihood ratio tests comparing full to reduced models to evaluate the statistical significance of the combined fixed effects (full model vs. a model including only the random effect) as well as each individual fixed effect (full model vs. a model in which that effect was removed). Pairwise contrasts for visual system were calculated using estimated marginal means, using the "emmeans" R package v. 1.8.2 (Lenth 2023). If we detected a significant interaction term, we ran separate models for each visual system, as well as a model including only chimpanzee and raptor visual systems. These models used the same approach but were fitted using the optim optimizer with the BFGS method, which resulted in better model convergence.

We analysed the ratio of false edges that run orthogonal to an animal's true outline using a linear mixed model, using the "lme4" package v. 1.1–34 (Bates et al. 2014) in R 4.3.1 and lmerTest v. 2.-29 to gain significance values (Kuznetsova et al. 2017). The edge disruption index (GabRat) was used as the outcome variable, and the modelled distance and its interaction with the visual system were used as explanatory variables, with image ID set as a random factor.

A phylogenetically controlled comparative analysis was conducted as a logistic regression in a Bayesian framework using the R package "MCMCglmm" v. 2.35 (Hadfield 2010). This model fitted the presence of black-and-white coloration (response) against the predictors of average adult body mass (g) and average social group size (fixed effects). Prior to model construction, species with missing data for the variables being tested were trimmed from both the dataset and the phylogeny. The phylogeny was accessed in R (v.4.3.0) via the use of package "phangorn" v. 2.11.1 (Schliep 2011). Priors for the regressions' fixed effects were assigned to each model using the command "gelman.prior." The residual variance was fixed at 1, and the phylogenetic variance was set to an improper prior ($V = 10–10$, $v = -1$) in all models, as is standard for this method. Using the current accepted mammal phylogeny, 100 tree topologies were selected at random before running each model, for use as random effects. A dummy run on an arbitrary tree preceded each model to determine the start point. These dummy runs ran for 11,000 iterations, with a burn-in of 1000 and a thin interval of 10. The models were then run across each of the 100 tree topologies for 11,000 iterations, with a burn-in of 1000 and a thin interval of 1,000, providing a total posterior sample of 1000 (10 per tree). Convergence of model parameters was checked via the Gelman-Rubin statistic (Gelman and Rubin 1992) (the potential scale reduction (PSR) factor among chains should be < 1.1; all PSR factors met this criterion). Variance inflation factors (VIFs) of the predictor variables were calculated for each multivariate model to check for multicollinearity between variables. All VIF values were below 10, allowing for independent interpretation of the results for variables in each of the models (O'Brien 2007).

Results

Colobus vellerosus showed substantial crypsis in their natural habitat, as measured by the proportion of the body that was chromatically indiscriminable from the background for the predator vision models used (i.e., felid, chimpanzee, raptor; Fig. 2). Across all visual systems and viewing distances, the mean proportion of the colobus monkey that overlapped with the background was 94.02% (± 10.86% standard deviation; range 49.53–100%); all visual system by viewing distance combinations had a mean proportion overlap of over 85% (Table 1; Fig. 3). In 60.31% of images, all colobus colours also existed in the background, yielding

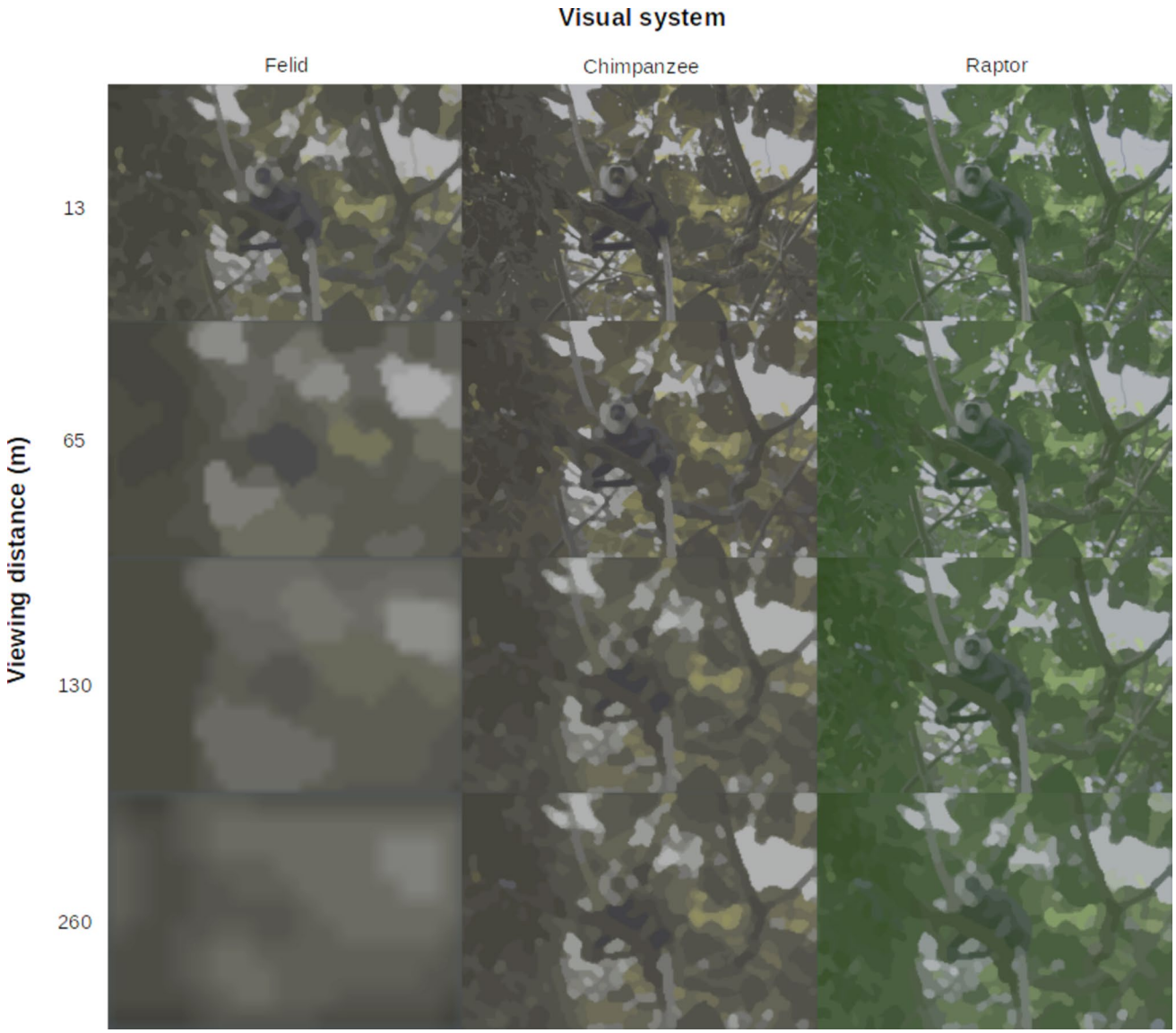

Fig. 2 A methodological example of visual modelling. Columns represent three visual systems (felid, chimpanzee, raptor) through which black-and-white colobus appearance was modelled in this study. Rows represent the increasing viewing distance (in meters)

Table 1 Mean ± standard deviation of colobus monkey crypsis, measured as the proportion of the body that was chromatically indiscriminable from the background, across visual systems and viewing distances

	Viewing distance			
	13 m	65 m	130 m	260 m
Felid	0.917 ± 0.123	0.915 ± 0.141	0.995 ± 0.041	1.000 ± 0.000
Chimpanzee	0.985 ± 0.043	0.939 ± 0.103	0.917 ± 0.113	0.907 ± 0.127
Raptor	0.982 ± 0.050	0.945 ± 0.091	0.907 ± 0.133	0.874 ± 0.134

comprehensive chromatic overlap between the colobus and the natural background.

Degree of colobus monkey crypsis varied across visual systems and distances. A model including visual system, viewing distance, size in frame, and occlusion was a better predictor of crypsis than a null model ($X^2 = 226.820$, $p < 0.001$). Animal size in frame (i.e., the proportion of the image area that included the colobus monkey) and occlusion (i.e., the proportion of the colobus monkey obscured by foliage) were not significant predictors of crypsis (respectively: $X^2 = 0.849$, $p = 0.357$; $X^2 = 0.147$, $p = 0.702$). There was a significant visual system by viewing distance interaction

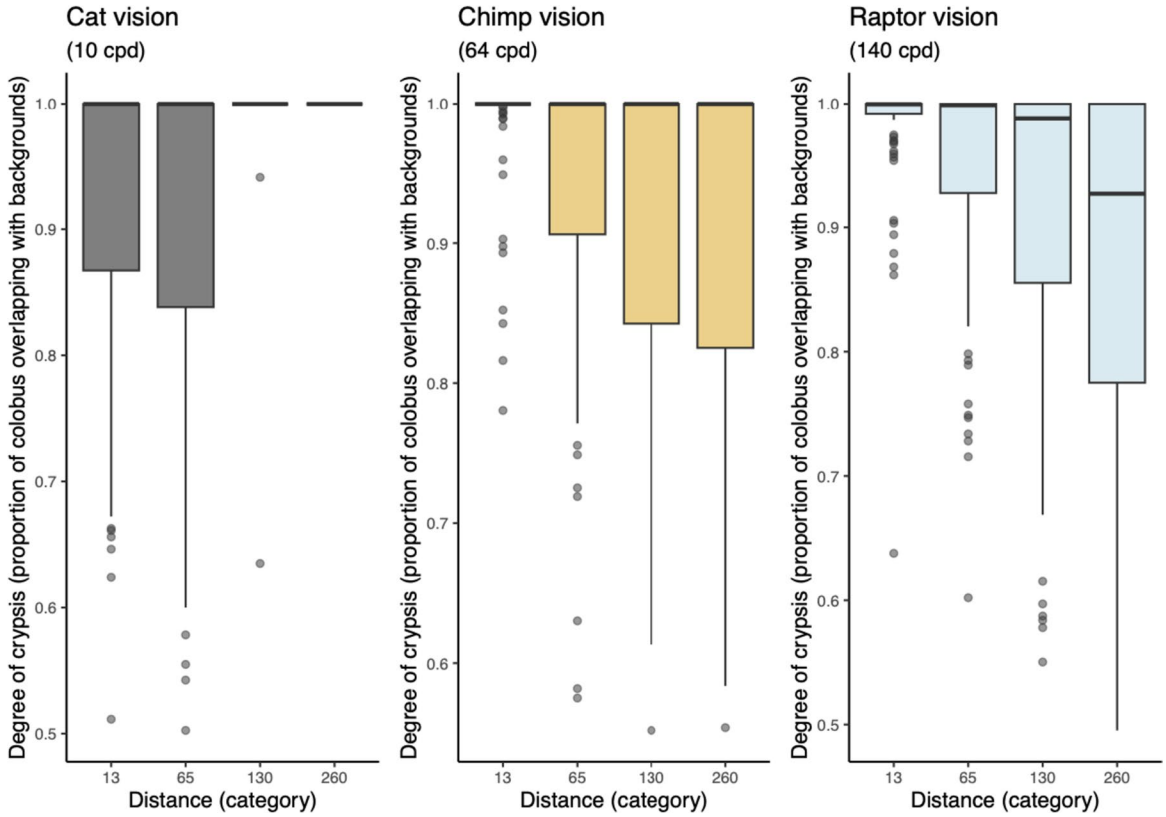

Fig. 3 Degree of crypsis in colobus monkeys across visual systems and viewing distances. The vision modelling was performed using acuity-corrected images: cat vision (10 cpd, i.e., cycles per degree), chimp vision (64 cpd), and raptor vision (140 cpd), the predator surrogates. The boxplot shows minimum and maximum (whiskers), median horizontal line, and the interquartile range of the simulated data. Outliers, depicted as individual dots beyond the whiskers, are values significantly deviating from the central tendency of the dataset

($X^2 = 67.784$, $p < 0.001$); therefore, we analysed crypsis as a function of viewing distance for each predator visual system separately. When perceived by felid predators, colobus monkey crypsis increased with viewing distance ($X^2 = 68.901$, $p < 0.001$), but when perceived by chimpanzees or by raptors, crypsis unexpectedly decreased with distance (chimpanzees: $X^2 = 48.114$, $p < 0.001$; raptors: $X^2 = 58.645$, $p < 0.001$). In an additional model of combined chimpanzee and raptor data, a visual system by viewing distance interaction was not significant ($X^2 = 0.245$, $p = 0.620$), and colobus monkey crypsis decreased with distance ($X^2 = 103.059$, $p < 0.001$) and the degree of crypsis was lower when viewed by raptors than chimpanzees ($X^2 = 30.474$, $p < 0.001$).

Edge disruption was poor at close proximity, compared to edge disruption measured further away. Edge disruption increased steeply with distance for dichromatic feline vision, after which it levelled out at longer distances (i.e., edge disruption, distance by vision model interaction; Fig. 4). Since there was a significant visual system by viewing distance interaction ($F_{2,160} = 39.49$, $p < 0.001$), we also analysed edge disruption as a function of viewing distance for each visual system separately. Edge disruption significantly increased over distance for chimpanzee vision ($t = 13.72$, $p < 0.001$) and feline vision ($t = 9.26$, $p < 0.001$). For raptors, edge disruption remained markedly low across increasing distances owing to birds' very high spatial acuity ($t = 1.21$, $p = 0.229$).

Lastly, we examined possible defences available to black-and-white colobus species in comparison to their nearest extant relatives, red and olive colobus species using phylogenetically controlled comparative analyses. Controlling for shared ancestry, we found no significant differences between black-and-white species and non-black-and-white species in regard to average body weights (averages, $N = 5$ black-and-white colobus species, 8.9 kg; $N = 7$ red or olive colobus species, 6.8 kg respectively; MCMCglmm $\beta = 0.1228$, $p = 0.920$) although average body weight was 30% larger in black-and-white species. Additionally, we found no significant difference in mean group size between the black-and-white species and the non-black-and-white species ($\beta = -0.6743$, $p = 0.890$).

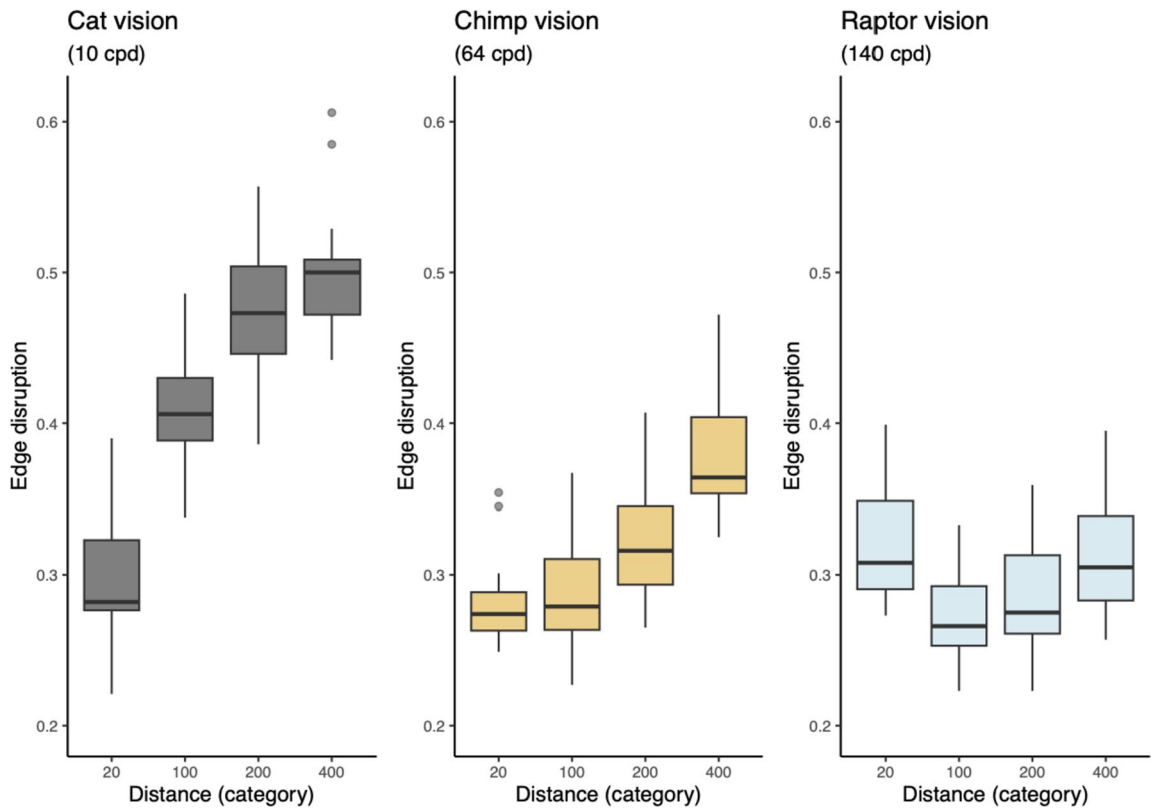

Fig. 4 Edge disruption of colobus monkeys across visual systems and viewing distances. The vision modelling was performed using acuity-corrected images: cat vision (10 cpd, i.e., cycles per degree), chimp vision (64 cpd), and raptor vision (140 cpd), the predator surrogates. The boxplot shows minimum and maximum (whiskers), median horizontal line, and the interquartile range of the simulated data. Outliers, depicted as individual dots beyond the whiskers, are values significantly deviating from the central tendency of the dataset

Discussion

Our findings support the idea that the appearance of colobus monkeys could serve as visually protective coloration. More specifically, we discovered that the black-and-white pelage of colobus monkeys, often conspicuous to human observers close-up, can facilitate blending in with background vegetation and patches of light at a distance as modelled through felid, chimpanzee, and raptor vision. This further suggests that black-and-white colobus pelage renders them cryptic against ecologically relevant receivers in their natural forest habitat.

Coloration that facilitates background matching should be a beneficial anti-predator adaptation for any animal (Cott 1940). In order to compare background matching against three ecologically different predators, we included a broad range of short to longer distances necessary for understanding how visual detection deteriorates by distance. We found that colobus animal-to-background similarity increased with distance when viewed by a low acuity ambush predator, such as cats. Plausibly, visual features of prey are easier for felid predators to perceive at close range and more difficult from further away as the target blends in with the background by distance (Barnett and Cuthill 2014; Nokelainen et al. 2021). Unexpectedly, when degree of crypsis (i.e., proportion of colobus colours found in the background) was measured through chimpanzee and raptor vision models, we found that crypsis declined with increasing viewing distance. One possibility is that for a high acuity predator, chromatic similarity of prey to its background may be counterintuitively high at close range but decrease by distance, as the spatial resolution of the background becomes more uniform when perceived further away. Additional research is needed to ascertain whether these reasonings are correct.

Intriguingly, contrasting colours may be an effective concealment strategy against multiple visual systems. Our edge disruption findings suggest that patterning of black-and-white colobus monkeys can be assumed to break up the boundary between the body and the background for felids and chimpanzees. In contrast, edge disruption did not increase with distance for raptors. To predators with relatively low spatial acuity, high contrast regions of small or distant prey will blend together and could effectively function as background matching. But to predators with higher spatial acuity, the same patterns may generate edge disruption and operate to break up the outline of the animal. Even

large patterns in large animals (such as colobus monkeys) could thus serve a disruptive function in habitats with similarly large pattern elements. High contrast body regions — like the black-and-white of colobus monkey's pelage — may therefore allow prey appearances to function differently across contexts, generating the potential for adaptation to a wider range of ecological conditions. Our results suggest that at a distance our focal species may gain visually protective benefits through background matching for felids, benefits through disruptive coloration for felids and chimpanzees, but rather little benefit via either mechanism against raptors. A comparative image analysis using many species with a spectrum of appearances would be helpful to assess ecological circumstances that facilitate black-and-white coloration, but this was beyond the scope of current work.

Controlling for phylogeny, although using a very small sample size, we found no evidence for black-and-white coloration being associated with large body size or large group size, both of which might be helpful in defence against predators. However, black-and-white colobus are 30% larger on average than their close relatives the red colobus and olive colobus, and it is extremely difficult to achieve statistical significance with small sample sizes (Santini et al. 2016; Lenzner et al. 2021). In a much larger sample across the primate order, black-and-white primates have been found to be significantly larger than non-black-and-white species, controlling for phylogeny (Howell et al. 2021). We therefore argue against dismissing the possibility that these large black-and-white colobines are advertising difficulty in handling due to body mass, at least to raptors where the predator–prey body size ratio is small.

Evidence is accumulating that mammalian pelage that appears striking to us is not necessarily conspicuous to ecologically relevant receivers (Caves et al. 2018). Our results are reminiscent of findings recently advanced to explain the black-and-white coloration of the giant panda which was found to be a form of both background matching and, at a distance, disruptive coloration when viewed through carnivore eyes (Caro et al. 2017; Nokelainen et al. 2021). Together with research on the function of black-and-white striping in zebras, which has shown that predators and parasites cannot resolve stripes unless they are very close up (Melin et al. 2016; How et al. 2020), we suspect this realization could help us investigate the visual function of coloration in other black-and-white mammals such as orcas and Malayan tapirs.

In summary, our study suggests that the appearance of black-and-white colobus monkeys' function to disguise this group of primates against several classes of predators. Whether black-and-white pelage additionally advertises large body size to some predators when viewed close-up is unresolved, but in the absence of additional evidence, our working hypothesis is that the black-and-white colobines are utilizing distance-dependent camouflage. They may be cryptic at a distance but more conspicuous (and signal difficulty in handling, which requires further evidence) close up to some predators (Barnett and Cuthill 2014). Finally, we acknowledge that although our focus here was on visual protective coloration, colours and pigments may serve other non-visual adaptive functions (e.g., pigment production, thermoregulation, immunocompetence), which are beyond the scope of this work; future research should address these possibilities to reveal the ultimate evolutionary drivers of conspicuous black and white coloration in mammals.

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Data availability Data analyzed during this study are included as supplementary files.

Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. Colobus monkeys were photographed opportunistically in natural forest settings during a behavioural ecology study with permission from the Ghana Wildlife Division, the management committee at Boabeng-Fiema Monkey Sanctuary, and the University of Calgary's Animal Care Committee. No animals were harmed during the photography.

Conflict of interest The authors declare no competing interests.

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