



The Evolutionary Ecology of Primate Hair Coloration: A Phylogenetic Approach

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Abstract

Understanding trait evolution is essential for explaining modern biological diversity, and this is particularly exemplified by studies of coloration. Recent studies have applied evolutionary models to understand animal coloration, yet we have limited knowledge of how this trait evolves in mammals in a comparative context. Here we use phylogenetic methods to examine how different traits are associated with the evolutionary diversity of primate hair color. We hypothesize that hair color evolves independently across body regions, and that variation in biological and ecological traits influence patterns of hair color evolution. To test this, we quantify the phylogenetic signal of coloration for each body region, then compare the fit of three evolutionary models and a null, non-phylogenetic model to explain color variation across 94 primate species. We then test how trait optima and rate of color evolution covary with biological traits, clade membership, and habitat. Phylogenetic signal varies across regions, with head and forelimb coloration exhibiting the highest values. Head and forelimb coloration is best explained by an Ornstein-Uhlenbeck model, which could suggest stabilizing selection, whereas a null model best fits other body regions. Rates of hair color evolution and optimal color values vary across species with different visual systems, activity patterns, habitat types, and clade memberships. These results suggest that selective pressures are acting independently across body regions and across different primate taxa. Our results emphasize the importance of investigating patterns of trait evolution across regions of the body, as well as incorporating relevant biological and ecological traits into evolutionary models.

Keywords Pelage · Pigmentation · Comparative methods · Mammal · Phenotypic divergence

Introduction

Examining how traits evolve is essential for understanding the diversity of organisms living today and in the past. Understanding the patterns of evolution that best explain trait diversity is a major topic within evolutionary ecology. Fortunately, the increasing availability of high-quality species-level phylogenies, comparative trait datasets across broad phylogenetic scales, and phylogenetic comparative methods (Butler and King 2004; Harmon et al. 2010; Revell

2012) are enabling scientists to quantify and analyze trait diversity in even greater detail.

One trait that has been the subject of several evolutionary studies is coloration. Evolutionary biologists have sought to understand variation in animal coloration since the beginning of the field (Darwin 1859; Wallace 1870) because coloration is a quantifiable, evolutionarily labile trait (Cuthill et al. 2017). Endler's (1980) foundational study on *Poecilia reticulata* color patterns demonstrated how competing selective pressures could differently shape various aspects of guppy coloration, and this line of inquiry continues today, particularly in birds (Stoddard and Prum 2008; Maia et al. 2013; Friedman and Remeš 2015; Marcondes and Brumfield 2019), squamates (Romero-Diaz et al. 2019; Allen et al. 2020), amphibians (Wang and Shaffer 2008; Nilsson Sköld et al. 2013), and fish (Seehausen et al. 1999; Nilsson Sköld et al. 2013). Recent comparative studies have examined interspecific variation in coloration in the context of species diversification, sexual selection, and covariation with other biological and ecological traits, such as habitat and visual

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system (Seehausen et al. 1999; Maia et al. 2013; Friedman and Remeš 2015; Bell et al. 2017; Allen et al. 2020). Studies of both bird and squamate coloration suggest that dorsal and ventral body surfaces are unevenly affected by the species' light environment (Marcondes and Brumfield 2019; Romero-Diaz et al. 2019; Allen et al. 2020). These existing vertebrate color studies demonstrate the role of ecology in rapidly shaping color evolution and variation, as well as the ability for selective pressures to differentially shape different parts of the body (Friedman and Remeš 2015; Bell et al. 2017; Marcondes and Brumfield 2019; Romero-Diaz et al. 2019).

Though our knowledge of vertebrate color evolution is growing, color evolution in mammals is comparatively understudied. A potential reason for the less frequent investigation of mammal color evolution is their relatively drab coloration compared to birds and other vertebrates. One mammalian order is a notable exception—Primates. Much of the research on primate hair color has focused on the genetic mechanisms regulating it, and the results of these studies illustrate the complexity of how variation in coloration has evolved across the primate order (Mundy and Kelly 2003; Haitina et al. 2007; Bradley et al. 2013; Tapanes et al. 2021). There also exists a productive body of research on the adaptive function of primate skin coloration, particularly focused on its use in social and sexual signaling (Henzi 1985; Waitt et al. 2003; Setchell 2005; Setchell et al. 2006; Bergman et al. 2009; Renoult et al. 2011; Cramer et al. 2013; Dubuc et al. 2014; Petersdorf et al. 2017). Nevertheless, the relative accuracy of primate phylogenies, along with the biological diversity found among primate lineages, makes primate hair color evolution a rich but understudied subject for broad comparative analyses (Fleagle et al. 2010; Kamilar and Cooper 2013). Primates exhibit an extraordinary degree of color variation across and within species, and in some cases show divergent color patterns among closely related species (Caro 2005; Bradley and Mundy 2008; Kamilar and Bradley 2011b). This high degree of color diversity may also be related to the fact that primates exhibit more variation in ecology, activity period, color vision, and social systems than the three other largest mammalian orders (Sumner and Mollon 2003; Bradley and Mundy 2008). Though researchers are far from fully understanding the intricate proximate and ultimate factors behind hair color diversity, existing studies have begun to identify the evolutionary forces shaping patterns of hair coloration in primates and other mammalian clades (Hoekstra 2006; Bradley and Mundy 2008; Santana et al. 2012).

Over the past two decades, a handful of studies using comparative phylogenetic methods have examined the ecological and biological factors driving color variation in various mammal clades, including carnivorans (Ortolani 1999; Caro et al. 2017a, b), cetaceans (Caro et al. 2011),

artiodactyls (Stoner et al. 2003), pinnipeds (Caro et al. 2012), and sciurids (Sheets and Chavez 2020). Comparative studies of primate coloration exist, but have typically been limited to exploring variation in facial coloration, which also include skin pigmentation in their analyses (Santana et al. 2012, 2013; Allen et al. 2014; Rakotonirina et al. 2017). The results of these existing studies demonstrate the adaptive function of hair color in background matching, thermoregulation, and both intraspecific and interspecific communication (Caro and Mallarino 2020). Nonetheless, these few aforementioned studies represent nearly the entirety of comparative phylogenetic analyses of mammal hair color evolution.

These existing studies demonstrate that multiple selective pressures and neutral processes can influence hair color diversity (Bradley and Mundy 2008; Hofreiter and Schöneberg 2010; Cuthill et al. 2017). Furthermore, these selection pressures may affect coloration in functionally divergent ways across regions of the body (Bradley and Mundy 2008; Santana et al. 2012). Concealment from other species is a common function of hair color. Background matching, countershading, and pattern blending can be achieved when pelage coloration and patterning resembles dominant environmental colors, or match patterns of light and dark in the habitat (Caro 2005; Bradley and Mundy 2008; Kamilar 2009; Kamilar and Bradley 2011a; Manceau et al. 2010). Hoekstra and Nachman's (2003) seminal study on melanism in pocket mice explored the genetic mechanisms behind color variation in populations of pocket mice, and tied these genetic mechanisms to adaptive, environment-dependent changes in hair color for the sake of background matching. Since then, research connecting genetic changes to environmentally adaptive shifts in hair color has steadily continued, particularly in mice (Hoekstra et al. 2004; Hoekstra 2006) but also in wolves (Anderson et al. 2009) and hares (Jones et al. 2018). Background matching may be one reason why species in forested environments tend to have darker pelages than species in more open environments (Kamilar and Bradley 2011b; Price 2017). Simultaneously, the degree of melanin in hair can also be physiologically adaptive, and assist in thermoregulation and protection against UV radiation (Caro 2005; Kamilar and Bradley 2011b; Santana et al. 2012). Hair coloration is also tied to conspecific communication. Unique patterns of hair color can serve as species-specific cues to help closely related species living in the same area distinguish each other and prevent deleterious hybridization (McNaught and Owens 2002; Santana et al. 2012; Allen et al. 2014; Martin et al. 2015; Price 2017). Particularly vibrant or melanistic hair patches may exploit female sensory preferences—as described by the sensory exploitation hypothesis (Ryan 1990; Schaefer et al. 2004; Fernandez and Morris 2007)—and might also signal to potential mates

the parasite load, hormonal levels, and overall quality of males (West and Packer 2002; Clough et al. 2009; Hofreiter and Schöneberg 2010).

Some of the biological traits that may influence hair color vary greatly across the three major primate clades (Sumner and Mollon 2003; Kamilar et al. 2013). For example, strepsirrhines (lemurs, lorises, galagos, and pottos) are small-bodied primates that are nearly all arboreal and have a reduced reliance on visual cues for intraspecific communication (Fleagle 2013). Though, these taxa show a variety of color vision phenotypes including dichromatic, monochromatic, and several polymorphic trichromatic lineages (Kawamura and Kubotera 2004; Valenta et al. 2016; Jacobs et al. 2019). Strepsirrhines also occupy a wide range of environments, from arid spiny forests to bushlands to tropical rainforests (Kappeler 2012). In contrast, members of the platyrrhine clade (monkeys of the Americas) are generally medium-sized, diurnal, and arboreal, though there are some notable exceptions to this pattern (Fleagle 2013). Platyrrhines are typically sex-linked polymorphic trichromats, though howler monkeys are universal trichromats and owl monkeys are monochromats (Jacobs 1993). The catarrhine primates (monkeys and apes of Africa and Asia) are all diurnal and universal trichromats (Jacobs 1993). Catarrhines occupy a wide range of habitats that vary greatly in their tree cover and light environment, with many species spending a substantial amount of time on the ground (Fleagle 2013). These biological traits may impose selective regimes on primate hair color that varies across body regions and across species.

With these various evolutionary processes and selective forces in mind, we use phylogenetic methods to examine patterns of hair color evolution across body regions for a wide array of primate species representing all major clades. Specifically, we ask the following questions: (i) does the phylogenetic signal of hair coloration vary across body regions, and (ii) what evolutionary models best explain hair color variation across different body regions. We hypothesize that hair color evolves independently across body regions. We predict differences in the strength of phylogenetic signal across body regions, as well as variation in which evolutionary model best explains patterns of hair color evolution across body regions. For body regions that may play a stronger role in conspecific and interspecific signaling, such as the head and tail, we predict a higher phylogenetic signal and either Ornstein-Uhlenbeck or Early Burst models as being the best fit model. For regions that may be important to background matching with environmental conditions, such as the torso, we predict a weaker phylogenetic signal and that the best-fitting model will be non-phylogenetic (null). If torso coloration is generally connected to crypsis, then we would expect torso color to have a relatively weak phylogenetic signal because closely related primate species frequently

inhabit different environments (Kamilar and Muldoon 2010; Kamilar and Cooper 2013).

We also investigate the importance of several key biological traits in guiding primate coloration. Specifically, we ask how (iii) variation in optimal trait values and (iv) variation in rates of evolution for hair coloration relate to differences in visual systems, activity patterns, habitat types, and clade designation (Strepsirrhini, Platyrrhini, Catarrhini). We also examine if major primate clades differ in the amount of hair color variation they exhibit, given broad differences in biological and ecological traits between strepsirrhines, catarrhines, and platyrrhines. Considering the findings from other vertebrate taxa, we hypothesize that variation in biological traits will affect the adaptive constraints and rates of hair color evolution. We predict that the selective regime of these traits will vary across body regions, reflecting differences in the functional significance of a body region's coloration (Butler and King 2004; O'Meara 2006).

Methods

Hair Color Data

Our data consist of RGB color value measurements from color calibrated digital photographs of preserved female museum skins from the American Museum of Natural History and the Field Museum of Natural History, using standard methods that have been tested for reliability and accuracy (Stevens et al. 2007; Kamilar and Bradley 2011b; Bergeron and Fuller 2018). These skins are carefully stored and are infrequently exposed to ambient light. The museum collections included both flat and stuffed skins; stuffed skins were photographed from multiple positions with each side of the skin facing the camera. We used a Canon Rebel XTI digital camera without flash, with the color mode set to 'faithful,' and with custom white balance. We then set the camera's white balance using an 18% gray card. An Xrite colorchecker card was placed next to each skin to allow for color correction. These settings were used to reduce color processing from the camera. All photography occurred with two external lights with tungsten bulbs pointed toward white umbrellas to produce indirect light across the entire specimen.

Photographs were recorded in RAW format then converted to linearized 16-bit TIFF files using the Canon Digital Photo Professional software. Within Adobe Photoshop, we used the Pictocolor plugin to standardize each image based on the known color values on the colorchecker card. These color-standardized images were resaved as TIFF files. We then measured RGB values from the color-standardized TIFF files by using the Eyedropper tool in Adobe Photoshop with a 5 × 5 pixel average. Anatomical landmarks on the

specimens were used to achieve uniformly positioned samples across species. We avoided sampling from specimens missing hair in these measured areas. With these methods, we measured 20 body locations (Fig. 1) for 145 individuals representing 94 primate species, with measurements per species coming from one to five female research skins selected based upon their condition. We subsequently grouped these 20 color measurements into five major body regions: the head, the torso, forelimbs, hind limbs, and tail.

RGB—red, blue, and green—is a type of color model with tristimulus color variables that can be used to accurately measure color values through proportions of green, red, and blue light (Hill and McGraw 2006). In a receiver-neutral RGB color space, hair color can vary along axes of relative red, green, and blue values, with a white coloration being the additive result of all three colors (Hill and McGraw 2006).

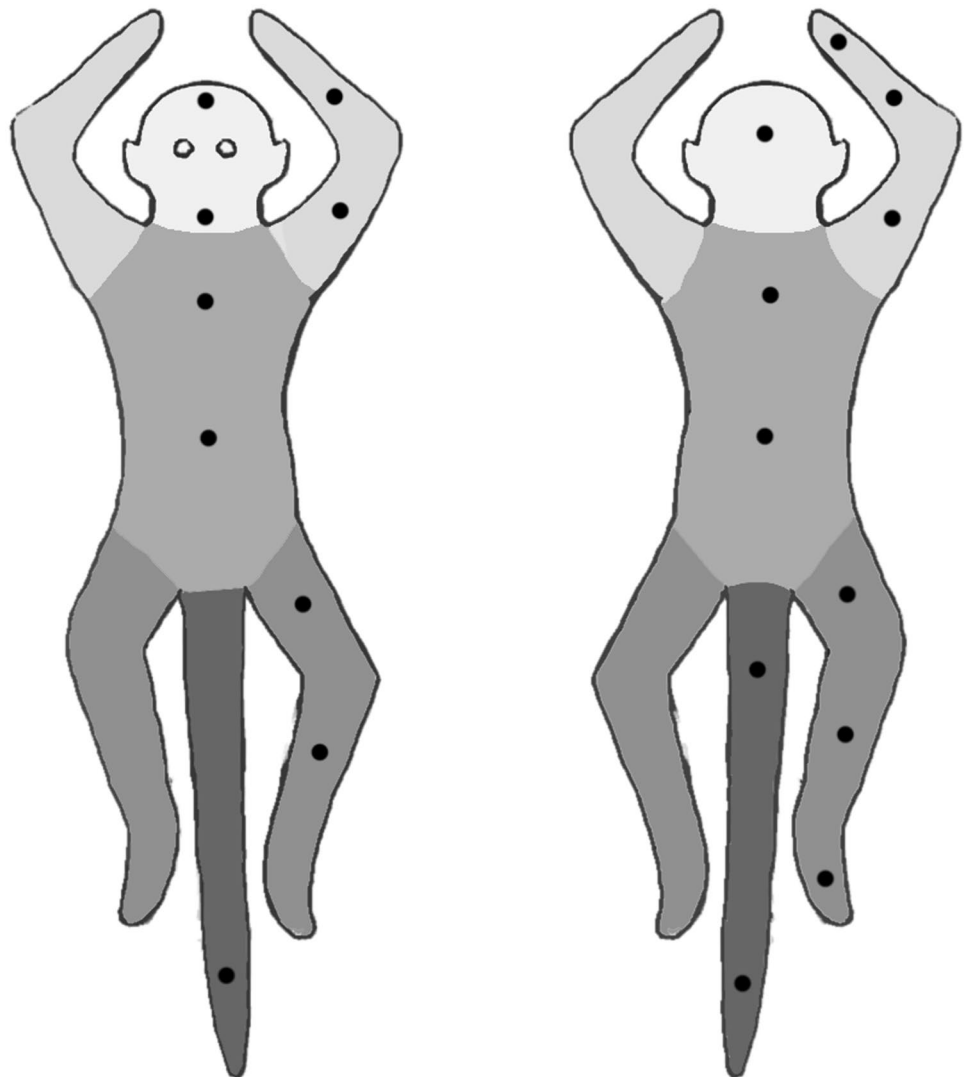
Several color value measurements within each body region are highly correlated with each other, which is

undesirable for our subsequent data analyses. Including multiple highly correlated variables in a principal components analysis may lead to inaccurate results if used for downstream statistical inference (McGarigal et al. 2000). Therefore, we removed variables with correlation coefficients over 0.9, and omitted any species with missing data for the given body region being analyzed. Due to the presence of zeroes within some individual color value measurements, we added a constant to all measurements (+0.01) and subsequently log-transformed the values to meet normal distribution assumptions for performing a PCA with the intention to use results in inferential statistics (McGarigal et al. 2000).

Multivariate Color Space

We conducted a principal component analysis (PCA) of RGB values for each body region based on a correlation matrix, using the `prcomp` function in R (R Core Team 2017). A RGB model is advantageous because it can be

Fig. 1 Sampling locations on primate museum research skins used to calculate RGB color values. Shading indicates the five major body regions these color measurements are grouped into: head, torso, forelimbs, hind limbs, and tail



used to quantify the major axes of primate hair color variation using linear variables: luminance (i.e., interpreted as the sum of RGB values) and redness (i.e., interpreted as the relative R and G values). The PCA allowed us to reduce dimensionality of the multiple color value measurements per body region. A standard PCA was used instead of a phylogenetic PCA because our goal was to examine variation in color space for a cross-species dataset (Rowan et al. 2016, 2020). In contrast, a phylogenetic PCA would quantify the differences in color space since the divergence of the taxa (Liam Revell pers comm.). In addition to reducing the dimensionality of our data, conducting these principal components analyses allowed us to determine how color values loaded onto each body region (see SI Table 1). Eigenvalues correspond to the magnitude of the principal components, and the variable loadings are the correlations between the original color measurements and the principal components. We then plotted the principal component (PC) scores generated by these PCAs to visually compare coloration in multivariate space for a given body region across all primate species in our data. These PC scores are representative of the RGB values for each body region, and were used in all further phylogenetic analyses (SI Table 1).

We also used the PC scores from PCA axis 1 and 2 to examine whether clades differed in the amount of color variation they exhibited for each body region. Because of the smaller strepsirrhine sample size ($n=24$) compared to catarrhines ($n=31$) and platyrrhines ($n=38$), we wanted to account for the potential effects of sample size on observed color variation. Therefore, we calculated the variance in PCA axis 1 and 2 scores for strepsirrhines, and accounted for the larger sample sizes in the two other clades by resampling each clade without replacement to generate a distribution of variances based on the number of strepsirrhine species. We used 1000 simulations and then compared the observed Strepsirrhini variance to the distribution of the simulated variances for PCA axis 1 and 2 at each body region. We considered strepsirrhines as showing significantly less color variation at a particular body region when their variance value was lower than 97.5 % of the simulated values for each of the other two clades.

To confirm the utility of using RGB color variation for quantifying hair luminance, we correlated our PC 1 scores with luminance values that we had simultaneously measured from the primate skins (using a hue/saturation/luminance color model). We ran a Spearman's rank correlation test between the PC1 scores and the luminance values for each body region using the `cor.test` function in R (R Core Team 2017). Spearman's rank correlation coefficient was chosen because it is a robust, non-parametric measure.

Phylogenetic Signal of Primate Hair Color

We used a consensus tree/chronogram from 10kTrees (Version 3) that represented the 94 primate species in our dataset (Arnold et al. 2010). This tree is based on sequence data from 11 mitochondrial segments and six autosomal segments taken from GenBank (Arnold et al. 2010). Five species were not available in the 10kTrees database: *Presbytis potenziani*, *Aotus miconax*, *Callicebus cupreus*, *Pithecia monachus*, and *Saguinus nigricollis*. For these species, we estimated the closest phylogenetic relationships of taxa in the phylogeny based on IUCN taxonomic information (Soul and Friedman 2015). We then manually added these species to the consensus tree in Mesquite 3.31 (Maddison and Maddison 2017), creating polytomies between the added species and their closest relatives. These polytomies were later randomly resolved in R using the `ape` package's `multi2di` function.

We used Pagel's λ to quantify phylogenetic signal in the resulting PC scores with the `phylosig` function in `phytools` for R (Pagel 1999; Münkemüller et al. 2012; Revell 2012). Using the `phylosig` function, we also conducted likelihood ratio tests to investigate whether phylogenetic signal was significantly greater than zero in each body region (Revell 2012). We only examined principal components with eigenvalues greater than one, which were PC1 for all body regions as well as PC2 for the torso. We recorded all PCA results, and plotted PC1 and PC2 as biplots to understand general trait patterns. These PC scores were also mapped as continuous trait values on the phylogenetic tree.

Modeling Hair Color Evolution

We used PC scores for each body region to assess three evolutionary models and a null model using default parameter settings: Brownian motion (BM), Early Burst (EB), and Ornstein-Uhlenbeck (OU), as well as a null white noise model that indicates a non-phylogenetic pattern. A BM model best fits a trait that has similar values among closely related species and divergent values between distantly related species due to a random walk of trait change over time—in other words, neutral evolution (Harmon et al. 2010). An EB model is one in which the trait changes rapidly in closely related species' early phylogenetic history, but slows down exponentially as the radiation continues over time (Harmon et al. 2010). Lastly, an OU model with a single stationary peak describes a trait undergoing stabilizing selection towards an optimum value across all species (Butler and King 2004). The fit of these evolutionary models was assessed with the `fitContinuous` function in `geiger` for R (Harmon et al. 2008; Pennell et al. 2014), which fit the likelihood of these models to the hair color PC data for each body region. We

compared the Akaike's Information Criterion (corrected for small sample size) values (AICc) between all models for each body region to determine the model of best fit, following the information-theoretic approach to multi-model selection (Burnham et al. 2011). If delta AICc values were less than 2 between the null model and a different evolutionary model, the null model could not be excluded as the best fit (Burnham and Anderson 2003).

The Role of Biological Traits in Shaping Optimal Values and Rates of Hair Color Evolution

We examined additional evolutionary models that allowed us to test for clade-specific and trait-specific variation in hair color evolution. All primate species were classified into the suborder Strepsirrhini ($n = 24$), the parvorder Catarrhini ($n = 31$), or the parvorder Platyrrhini ($n = 38$). *Tarsius syrichta* is not a member of these clades and was therefore excluded from this component of our analysis. For each body region, we used the mvOU function from the *mvMORPH* R package (Clavel et al. 2015) to compare OU evolutionary models with a single trait optimum for all clades to OU models with a different optima for each clade (i.e., multiple selective regimes). This function calculates the log-likelihood of each model, the trait optima parameter θ , the selection strength parameter α , the random drift parameter σ , and the AICc which we used to determine the model of best fit. We then compared the probability of a single evolutionary rate vs. clade-specific rates of evolution (following Brownian motion) for each body region via a likelihood ratio test. These tests were conducted using the *brownie.lite* function from the *phytools* R package (Revell 2012), which calculates the parameter σ^2 (degree of drift and distribution of phenotypic states for a trait), the selection strength parameter α , the log-likelihood of the single-rate and multiple-rate models, and the P-value for the likelihood ratio test.

These analyses were repeated for three different categorical traits other than clade: visual system, activity pattern, and habitat type. The visual system of each species included in this study was classified as “trichromat,” “polymorphic,” “dichromat,” or “monochromat.” These classifications were based on comparative datasets on color vision and opsin variation in primates (Tan and Li 1999; Kamilar et al. 2013; Veilleux et al. 2014; Valenta et al. 2016; Jacobs et al. 2019). The activity pattern of each species was classified as either “diurnal,” “cathe-meral,” or “nocturnal” and was based on a dataset from Kamilar et al. (2013). We re-ran these analyses using the dichotomous classification of “low-light” vs. “diurnal” because of the relatively small number of species classified as “cathe-meral” in our dataset, but this did not significantly alter the results. The results reported are therefore from the original “diurnal,” “cathe-meral,” and “nocturnal” classification system. Lastly, we classified the habitat type

of each species as either “wet,” “moderate,” or “dry.” These classifications were based on continuous, averaged actual evapotranspiration (AET) values compiled in Kamilar et al. (2013) within the ranges of primates included in this dataset. AET was chosen to define our habitat categories because of its potential selective pressure upon hair coloration (Gloger 1833; Kamilar and Bradley 2011b; Ribot et al. 2019). These values were compared with habitat composition descriptions for each species from the All the World's Primates global database to determine ecologically significant categorical cutoffs of these AET values (Rowe and Myers 2017). Primate species with habitat AET values above 1,200 were classified as “wet”; primate species with habitat AET values between 1,010 and 1,200 were classified as “moderate”; and primate species with habitat AET values below 1,010 were classified as “dry.” All phylogenetic analyses were conducted in R, using the *mvMORPH*, *phytools*, *geiger*, *ggplot2*, *phangorn*, and *ape* packages (Harmon et al. 2008; Wickham 2009; Schliep 2011; Revell 2012; Pennell et al. 2014; Clavel et al. 2015; Paradis and Schliep 2019).

Data Availability Statement

The datasets generated and analyzed during the current study are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.dbrv15f16>.

Results

Multivariate Color Space

Bi-plots of the body region-specific principal component analyses reveal largely overlapping multivariate space among major taxonomic groupings (Fig. 2). Nonetheless, some patterns of color variation emerge across Strepsirrhini, Catarrhini, and Platyrrhini. Throughout the bi-plots in Fig. 2, PC1 represents pigmentation variation from eumelanin-dominant dark colors to bright, pheomelanin-dominant or lightly pigmented colors. This was confirmed by examining the variable loadings for PC1 across body regions, as well as the correlation analysis between PC1 scores and the multiple luminance values for each body region (SI Table 2). RGB is an additive color space, with white being the product of all three colors. Variable loadings show that PC1 is positively associated with an increase in red, blue, and green color channels. A correlation test between PC1 scores and the raw luminance values demonstrated that PCA axis 1 has a positive, statistically significant correlative relationship with luminance (dark to light values in hair). The variable loadings for PC2 vary more between bi-plots, but generally represent patterns of contrasting coloration within each body region.

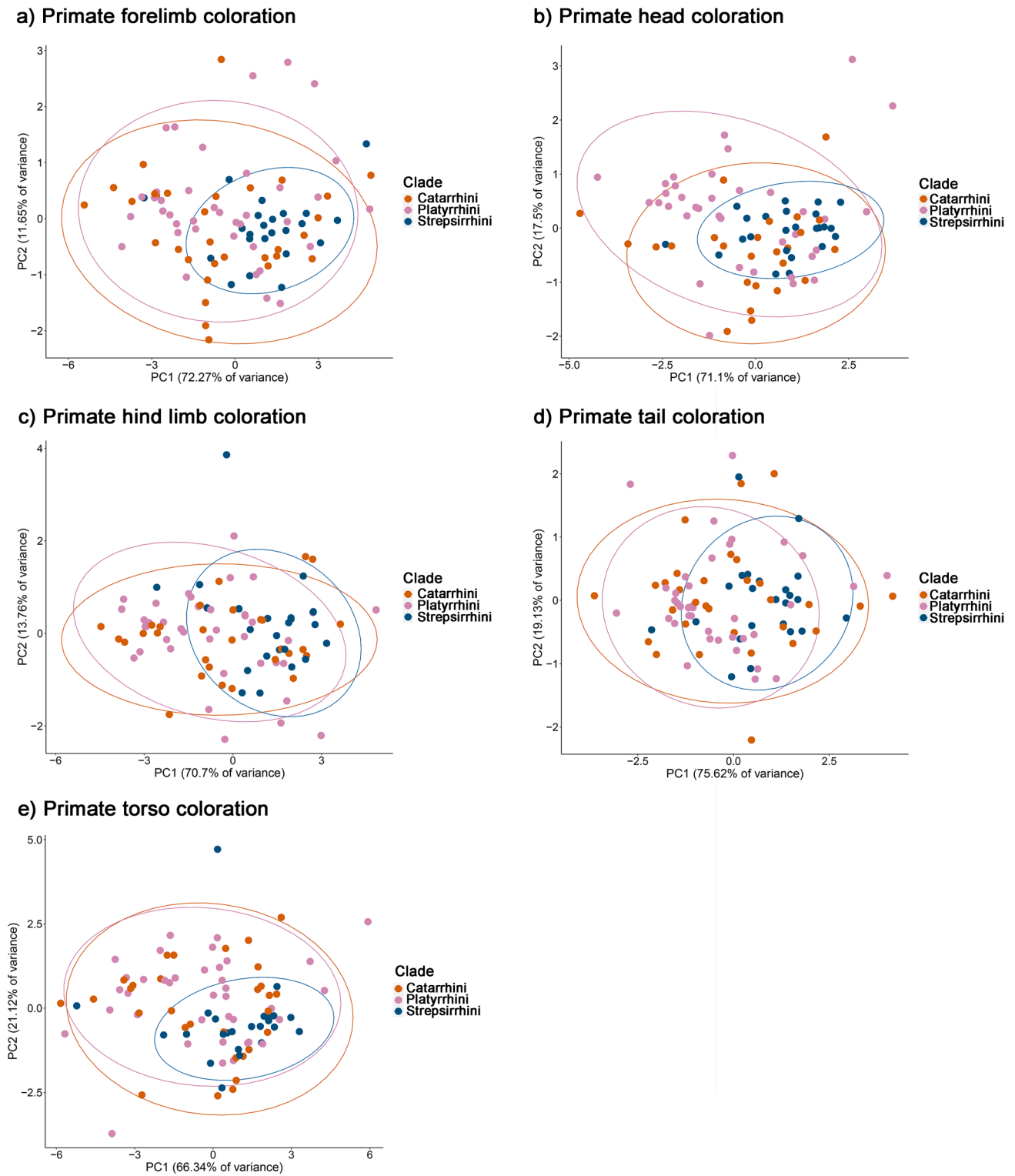
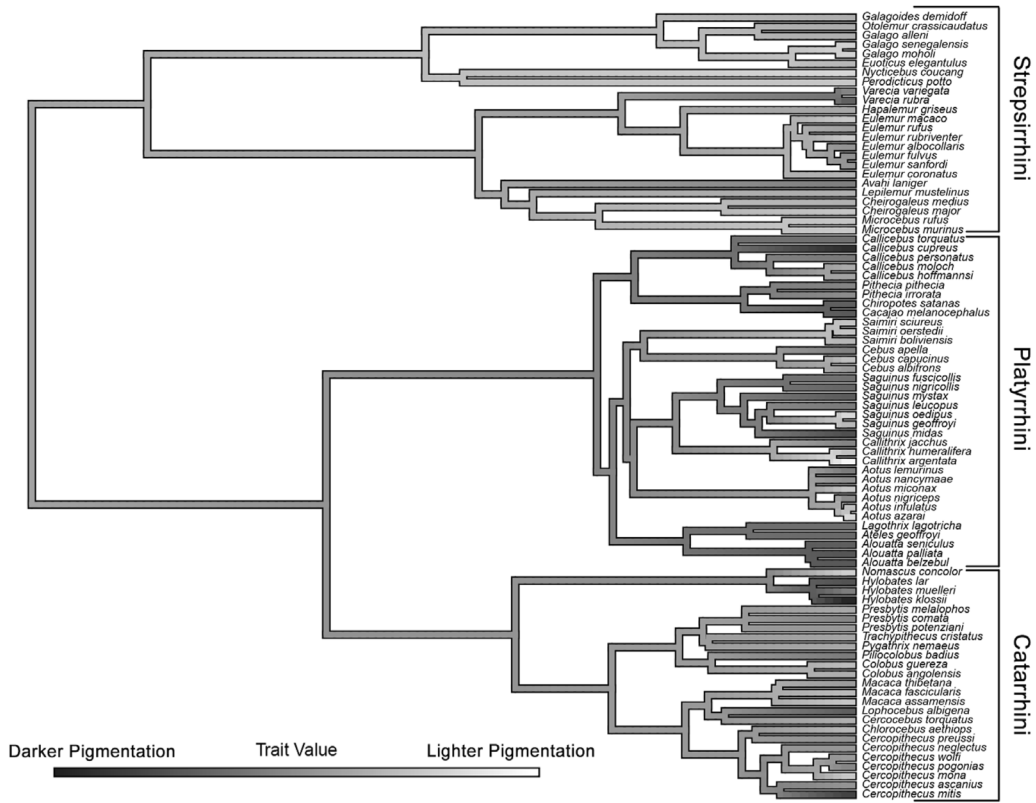


Fig. 2 The first two components of body region-specific RGB principal component analyses across all primate species in the study (for which the specific body color data were available). The suborder Strepsirrhini and parvorders Platyrrhini and Catarrhini are delineated by a 95% confidence interval drawn around each clade. The Strepsirrhini tend to exhibit less color variation than other primate clades

a) Primate head color



b) Primate forelimb color

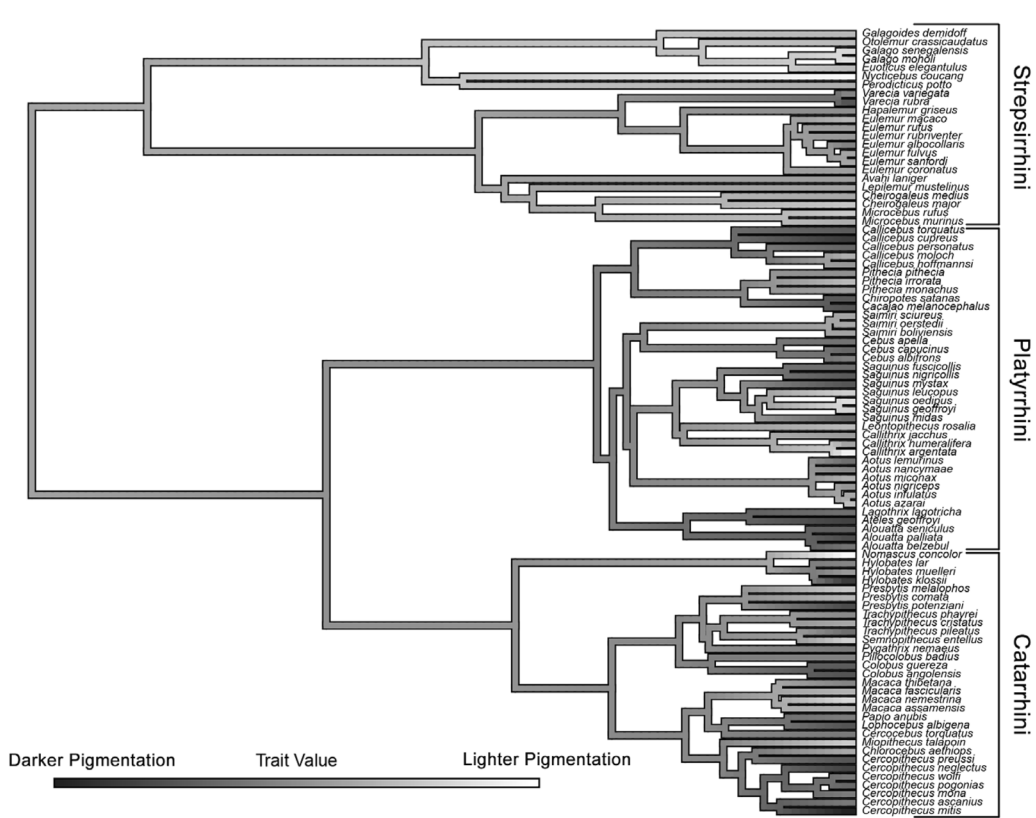


Fig. 3 Variation in (a) head and (b) forelimb PC1 values generated from RGB data, mapped on the primate phylogenetic tree. Black indicates darker coloration and an increase of eumelanin; white indicates lighter pigmentation

For both head and forelimb coloration (Fig. 3a and b, respectively), platyrrhine and catarrhine trait variation seems similarly diverse. Strepsirrhine PC scores have a consistently smaller distribution along both axes, suggesting less overall interspecific color variation than present in catarrhines and platyrrhines. Strepsirrhine variation is instead limited to a smaller multivariate space that is almost entirely encompassed within the range of both catarrhines and platyrrhines. Furthermore, the range of Strepsirrhini PC scores are generally grouped toward the right side of the horizontal axis, indicating a slightly more lightly pigmented coloration within the suborder.

For virtually all body region and clade comparisons along the PCA axis 1—which explains more than three times the variation in hair color compared to PC2 across body regions—we found that observed strepsirrhine variances fell below the 97.5% distribution of simulated subset catarrhine and platyrrhine variances. Observed strepsirrhine variance in tail color was the only exception when compared to simulated platyrrhine variances, as it fell just within the 95% distribution of simulated platyrrhine variances. Results were more mixed for PCA axis 2: strepsirrhines had significantly lower variance compared to catarrhines and platyrrhines for the head and forelimbs, but did not fall outside of the 97.5% distribution of simulated catarrhine or platyrrhine variances for the tail or torso. Additionally, the observed strepsirrhine variance along PC2 for the forelimbs was higher than the 97.5% distribution of simulated catarrhine variances, and did not fall outside of the simulated platyrrhine variances.

Phylogenetic Signal of Primate Hair Color

We found significant phylogenetic signals for hair coloration in multiple body regions (SI Table 3). The head has the highest significant value of Pagel's λ at 0.468. Forelimbs and hind limbs also had significant λ values of 0.36 and 0.275, respectively. In contrast, the torso PC1 and tail had relatively low phylogenetic signals of 0.113 and 0.19, respectively—though the phylogenetic signal for tail coloration approaches significance ($p = 0.071$). While torso PC2 had a moderate λ value of 0.489, this value was not significantly different from 0.

Modeling Hair Color Evolution

When we modeled trait evolution across all 94 primate species, we found that head and forelimb color are both best explained by an OU model of evolution (Table 1 and

SI Table 4). The BM and EB models exhibited substantially less support with delta AICc values of at least 38. In all other body regions, color variation is equally fit (within 2 AICc values) by a white noise model of evolution and the OU evolutionary model. For these body regions, the BM and EB models were associated with delta AICc values of at least 43.

The Role of Biological Traits in Shaping Optimal Values and Rates of Hair Color Evolution

Several patterns emerge in our trait-specific evolutionary models. Across body regions, evolutionary models simulating multiple optimal coloration values defined by trait classification generally outperform evolutionary models with a single optimum (Table 1 and SI Table 5). Optimal color values (indicated here by the parameter θ , and representing the optimal value along PCA axis 1 for each body region) vary depending on body region and the trait classification used. Though, across nearly all body regions, primates classified as strepsirrhine, dichromat/monochromat, nocturnal, and/or living in dry habitats have a lighter optimal color value than other groups.

In terms of the rate of color evolution, at least one of the multiple evolutionary rate models performed better than the single rate model for each body region (Table 1 and SI Table 6). There was also variation across body regions in which trait-specific models performed better than single-rate models. For the forelimbs, a model with multiple, visual system-specific evolutionary rates and a model with multiple, habitat-specific evolutionary rates outperformed single-rate models to explain color variation. Head coloration was best fit by three out of the four trait-specific multiple rate models when compared to the single-rate model. Models of activity pattern-specific evolutionary rates and habitat-specific evolutionary rates explained hind limb coloration better than single-rate models. Clade-specific evolutionary rates and visual system-specific evolutionary rates best described observed tail coloration in primates. Conversely, only the habitat-specific multiple rate model outperformed the single rate model in torso coloration.

Discussion

Coloration is a particularly labile trait shaped by both natural and sexual selection along multiple axes of variation (Maia et al. 2013; Dunn et al. 2015). Our results underscore the complex evolution of primate hair variation. Primate hair color evolves differently across body regions, and seemingly independently between forelimbs and hind limbs. In addition, patterns and rates of hair color evolution vary across clades and species with different visual systems, activity

Table 1 Summary of phylogenetic signal (*Pagel's* λ) and evolutionary modelling results for hair color in multivariate (PCA) space per body region across 94 primate species^a. For full modelling parameters and values, see SI Tables 3, 4, 5, and 6

Body Region/PC	Pagel's λ^b	Evolutionary Model of Best Fit ^c	Trait-specific Optima (Θ) ^d Models Outperforming Single Optimum Model	Trait-specific Evolutionary Rate (σ^2) ^e Models Outperforming Single Rate Model
Forelimbs PC1	0.360	OU	<i>Clade</i> Catarrhini = -0.390 Platyrrhini = -0.631 Strepsirrhini = 1.340 <i>Visual System</i> Trichromat = -0.462 Polymorphic = -0.726 Dichromat = 0.993 Monochromat = 2.094 <i>Activity Pattern</i> Diurnal = -0.586 Cathemeral = 0.400 Nocturnal = 1.679 <i>Habitat</i> Dry = 2.420 Intermediate = 1.322 Wet = -0.558	<i>Visual System</i> Trichromat = 0.593 Polymorphic = 0.599 Dichromat = 0.119 Monochromat = 0.659 <i>Habitat</i> Dry = 0.067 Intermediate = 1.329 Wet = 0.482
Head PC1	0.468	OU	<i>Clade</i> Catarrhini = -0.114 Platyrrhini = -0.783 Strepsirrhini = 0.904 <i>Visual System</i> Trichromat = -0.306 Polymorphic = -0.809 Dichromat = 0.832 Monochromat = 1.128 <i>Activity Pattern</i> Diurnal = -0.554 Cathemeral = 0.881 Nocturnal = 1.015	<i>Clade</i> Catarrhini = 0.333 Platyrrhini = 0.493 Strepsirrhini = 0.117 <i>Visual System</i> Trichromat = 0.304 Polymorphic = 0.336 Dichromat = 0.081 Monochromat = 0.628 <i>Habitat</i> Dry = 0.005 Intermediate = 1.670 Wet = 0.229
Hind limbs PC1	0.275	Null	<i>Clade</i> Catarrhini = -0.322 Platyrrhini = -0.806 Strepsirrhini = 1.219 <i>Visual System</i> Trichromat = -0.453 Polymorphic = -0.783 Dichromat = 1.004 Monochromat = 1.459 <i>Activity Pattern</i> Diurnal = -0.640 Cathemeral = 0.873 Nocturnal = 1.423 <i>Habitat</i> Dry = 2.404 Intermediate = 0.592 Wet = -0.480	<i>Activity Pattern</i> Diurnal = 0.506 Cathemeral = 2.099 Nocturnal = 0.160 <i>Habitat</i> Dry = 0.087 Intermediate = 1.226 Wet = 0.453

Table 1 (continued)

Body Region/PC	Pagel's λ^b	Evolutionary Model of Best Fit ^c	Trait-specific Optima (Θ) ^d Models Outperforming Single Optimum Model	Trait-specific Evolutionary Rate (σ^2) ^e Models Outperforming Single Rate Model
Tail PC1	0.190	Null	<i>Clade</i> Catarrhini = -0.115 Platyrrhini = -0.373 Strepsirrhini = 0.793 <i>Activity Pattern</i> Diurnal = -0.257 Cathemeral = 0.726 Nocturnal = 0.672 <i>Habitat</i> Dry = 1.211 Intermediate = 0.170 Wet = -0.201	<i>Clade</i> Catarrhini = 0.325 Platyrrhini = 0.450 Strepsirrhini = 0.164 <i>Visual System</i> Trichromat = 0.304 Polymorphic = 0.392 Dichromat = 0.065 Monochromat = 0.550
Torso PC1	0.113	Null	<i>Visual System</i> Trichromat = -0.492 Polymorphic = -0.521 Dichromat = 0.728 Monochromat = 1.410 <i>Activity Pattern</i> Diurnal = -0.082 Cathemeral = -0.229 Nocturnal = -0.613 <i>Habitat</i> Dry = 2.428 Intermediate = 0.418 Wet = -0.365	<i>Habitat</i> Dry = 0.133 Intermediate = 2.280 Wet = 0.721
Torso PC2	0.489	Null	NA	NA

^a PC2 scores were included in analyses when its eigenvalue > 1

^b Phylogenetic signal is reported here using Pagel's λ . Bolded values indicate a λ significantly above 0 (P-value < 0.05)

^c Models of best fit were determined using AICc scores. OU stands for an "Ornstein-Uhlenbeck" model and the null model is non-phylogenetic

^d Θ represents the optimum PC1 value for primate species with a given trait

^e σ^2 represents the degree of drift and distribution of phenotypic states for primate species with a given trait

patterns, and habitat types. We suggest that these results are a function of selective pressures acting independently across body regions, as well as across different primate taxa. Our data support the idea that overall body color does not evolve as an integrated unit, but that body region coloration varies independently and likely serves different functions.

Clade Level Differences in Multivariate Color Space

Hair color diversity is much greater in catarrhines and platyrrhines compared to strepsirrhines, which may illustrate differences in evolutionary lability and potential selective forces among these clades. For example, catarrhine and platyrrhine primates are nearly exclusively diurnal—in stark contrast to strepsirrhines—which suggests a possible relationship between color variation and activity pattern that has been supported in a study of avian plumage color space (Stoddard and Prum 2011). The high visual acuity and color differentiation afforded by light-rich conditions (Sumner and Mollon 2003) mean that diurnal activity patterns may strongly affect hair

color evolution. Additionally, the wider spectrum of colors detected by routinely trichromatic catarrhines and polymorphic trichromatic platyrrhines may influence the adaptive range of pelage coloration for these clades (Sumner and Mollon 2003; Price 2017).

In contrast to monkeys and apes, ancestral lemurs were likely nocturnal and solitary, in which case routine monochromacy or dichromacy—depending on environmental light conditions—would be expected rather than polymorphic trichromacy (Kawamura 2016). Though there are multiple diurnal and at least one cathemeral lemuriform species with polymorphic trichromacy (Kawamura 2016; Jacobs et al. 2017), it is possible that the small range of multivariate space occupied by strepsirrhines does not reflect relatively recent color vision and activity pattern changes in lemuriform evolutionary history (Hall et al. 2012; Kawamura 2016). Instead, relatively limited strepsirrhine coat coloration may be connected to the ancestral strepsirrhine light conditions and greater reliance on non-visual modes of communication (delBarco-Trillo et al. 2011).

Phylogenetic Signal of Primate Hair Color

The strength of phylogenetic signal for hair coloration across all body regions is relatively low: out of the statistically significant phylogenetic signals, only head coloration has a Pagel's λ value greater than 0.4. This indicates that it is likely for distantly related species to converge on the same hair color phenotype and/or for closely related species to differ. The universally weak phylogenetic signal we found in primate hair coloration is in line with our previous research showing that the degree and pattern of melanism in primates is frequently adapted to ecological and behavioral variables (Kamilar and Bradley 2011a, b; Kamilar and Cooper 2013), which can often vary within a genus. Convergent evolution due to similar selective pressures and adaptive phenotypic solutions may indeed explain much of the low phylogenetic signal observed in this study. Additionally, weak phylogenetic signals for hair color are consistent with the current knowledge that pelage phenotypes can be markedly altered by multiple simple genetic mechanisms, providing more opportunities for convergent hair color phenotypes to emerge in different clades (Hoekstra 2006; Haitina et al. 2007; Bradley and Mundy 2008; Hofreiter and Schöneberg 2010). Empirical support for the evolutionary lability of primate coloration has multiple implications. A trait with phylogenetic signal approaching or equal to a λ value of 1 would be ideal for inferring phylogenetic relationships, but a lower phylogenetic signal indicates divergence and/or convergence of trait values unrelated to phylogenetic relationships (Pagel 1999). Therefore, researchers should be careful when using primate hair color to distinguish taxa. Due to the low phylogenetic signal present in torso, tail, and hind limb color, we suggest that researchers exercise particular caution when using these phenotypes to define or identify taxa. The relatively higher and statistically significant phylogenetic signal present in head and forelimb coloration indicate trait similarity across species less than would be expected under pure Brownian motion, but more than expected by chance alone. Therefore, pelage-based classification could depend more on these particular body regions than others, while still acknowledging the overall lability and non-Brownian motion of hair color evolution.

Modeling Hair Color Evolution Across Primates

Evolutionary modelling across primates revealed two major patterns: head and forelimb hair coloration best follow an Ornstein-Uhlenbeck model of evolution, whereas torso, hind limb, and tail hair coloration are not well described by phylogenetic models. Variation in primate head and forelimb coloration are indicative that both regions are the product of stabilizing selection toward adaptive peaks. This pattern is explained by their anterior position on the primate body (Caro

et al. 2017a) and their role in intraspecific and interspecific signaling, which could constrain variation in color. Under the sensory exploitation hypothesis, there would be a selective regime towards hair color values exploiting pre-existing female sensory preferences in body regions involved in sexual signaling (Ryan 1990; Schaefer et al. 2004; Fernandez and Morris 2007). These results may support the existing research on the use of primate facial coloration for species recognition, social communication, and sexual signaling (Clough et al. 2009; Santana et al. 2012, 2013; Allen et al. 2014). We note that Cooper et al. (2016) argued that OU models should be interpreted with caution because they are often associated with increased Type I errors when tree size is small. We agree with their general findings, though it is important to consider that when hair color variation was best fit by an OU model, they performed substantially better than the second best model according to delta AICc values.

Our results from modeling primate hind limb, torso, and tail color variation suggest that coloration in these body regions is unrelated to phylogenetic relationships. Incorporating biological traits into models of hair color evolution can therefore be particularly illuminating for these body regions.

The Role of Biological Traits in Shaping Optimal Values and Rates of Hair Color Evolution

Primates exhibit a range of biological traits that potentially shape the evolution of hair color. The high diversity of visual systems, activity patterns, and habitats occupied by primates may therefore impose heterogeneous—and even divergent—selective pressures on coloration. For these reasons, it is important to model these traits as selective regimes potentially shaping the rate and optimal values of hair color evolution.

The trait optima (θ) for coloration, as captured by PC1, reveal consistent trends. Across models with different selective regimes, strepsirrhines, dichromats/monochromats, nocturnal species, and species living in drier habitats have lighter-pigmented optimal values. Though this suite of traits may be somewhat correlated, they frequently occur separately from each other within the primate order: there is a great deal of habitat variation within clades, and even wide variation in activity patterns and color vision across the strepsirrhines included in this study. In contrast, platyrrhines, catarrhines, trichromats and polymorphic trichromats, diurnal species, and species living in wetter habitats tend to have darker to intermediate optimal values. We suggest that the selective regime of this first suite of traits pulls coloration toward a less melanistic, lighter coloration, whereas the selective regime of this second broad suite of traits may move hair color toward intermediate eumelanin levels. Figure 3 illustrates the presence of multiple

coloration optima across primates that follow this general pattern. Dichromatic and monochromatic strepsirrhine PC scores all tend to be lighter colored and also have little variation between lineages, with the polymorphic and diurnal ruffed lemurs clearly standing out within the clade. For strepsirrhine lineages and other lineages with limited color vision who are active in low-light conditions, pheomelanin-rich coloration may be less important in social signaling than eumelanistic contrast between different body regions (i.e., light and dark). Conversely, Fig. 3 shows the relative diversity of color ranges in both platyrrhines and catarrhines, with closely related species frequently differing greatly in their darkness. The prevalence of diurnal activity patterns, trichromacy in catarrhines, and polymorphic trichromacy in platyrrhines may increase the range of coloration useful in visual signaling (Kamilar et al. 2013). Different factors could be at play within each clade: while the wide variety of habitats inhabited by catarrhines could be influencing their range of head and forelimb coloration, the diversity of color vision systems in platyrrhines could also be driving their range of coloration and lead to an overall intermediate θ .

Though multi-rate models of color evolution generally performed better than single rate models across all body regions, the differences between body regions provide insight into the selective regimes shaping them. Models with visual system-specific evolutionary rates performed better than single rate models in forelimb, head, and tail coloration. Dichromats had the lowest rate of color evolution across all three body regions, whereas monochromats had the highest evolutionary rates. These results may suggest that the conspecific perception of hair color exerts stronger selection on these key regions of the body compared to the torso and hind limbs. The role of tail or rear color in conspecific communication has been supported by previous research (Caro 2008), and can facilitate social cohesion by making it easier for individuals to follow one another (Ortolani 1999). The rapid diversification and specialization of facial coloration recorded in multiple primate lineages (Santana et al. 2012; Allen et al. 2014; Rakotonirina et al. 2017) strongly suggest that this body region is a focal point within conspecific and interspecific signaling. Taken together, it would seem that the range of color values perceptible by conspecifics shape coloration in these body regions.

An activity-pattern specific model of evolutionary rate performed better than a single rate model only in hind limb coloration, with cathemeral species having a notably faster rate of evolution ($\sigma^2 = 2.099$) compared to nocturnal ($\sigma^2 = 0.160$) and diurnal species ($\sigma^2 = 0.506$). Though the functional significance of hind limb coloration is not clarified by this result, it does illustrate that hind limb and forelimb coloration clearly exhibit different evolutionary patterns and likely different functions. This result therefore suggests that selective pressures and/or genetic mechanisms

differ between hind limbs and forelimbs in primates. Therefore, further investigations into gene expression patterns across body regions could have important implications for explaining macroevolutionary patterns in primates and other animals.

Models of habitat-specific evolutionary rates performed well in all body regions except for the tail. These results align with general selective pressures toward cryptic coloration (Bradley and Mundy 2008). Notably, this was the only multi-rate model that performed better than the single rate model in torso coloration. This suggests that habitat type is the most important selective regime for shaping torso coloration in primates, and remains important throughout most regions of the body. Our results may support the light environment hypothesis, which posits that coloration is influenced by the type of light environment inhabited by the species (McNaught and Owens 2002). Studies in *Artodactyla* (Stoner et al. 2003) and *Carnivora* (Caro et al. 2017b) have demonstrated that torso coloration often has background matching functions guided by ecological factors, and our results provide initial evidence that primate torso coloration is similarly shaped by their habitat. There is evidence across both primate and avian species that variation in torso brightness and plumage coloration, respectively, follows Gloger's rule, which posits that species occupying warm and wetter environments tend to have a darker coloration (Gloger 1833; Kamilar and Bradley 2011b; Ribot et al. 2019). Under the assumptions of both the light environment hypothesis and Gloger's rule, species occupying similar habitats should exhibit similar coloration for the torso independent of their phylogenetic relationships. Given the results of this and other mammal coloration studies, the evolution of torso coloration in terrestrial mammals appears to be frequently determined by ecological factors. Our results further support the importance of a species' habitat in shaping their coloration, independent of the coloration of closely related species.

Several recent studies exploring rates of trait evolution and ecological differentiation have demonstrated a strong relationship between faster evolutionary rates and the strength of natural selection leading to adaptive ecological divergence (Baker and Venditti 2019; Crouch and Ricklets 2019; Luzuriaga-Aveiga and Weir 2019). For example, Baker and Venditti (2019) found that rapid rates of evolution in mammalian eye morphology were largely associated with changes in activity patterns over mammal evolutionary history. Faster rates of color evolution in cathemeral species and monochromats could therefore be a reflection of shifts to these activity pattern and color vision traits, with relatively recent shifts to cathemerality in some strepsirrhines and monochromacy in *Aotus* species driving this pattern. These evolutionary rate results more broadly demonstrate the concept that a change in one trait may trigger relatively rapid evolution in another, correlated trait.

Conclusions

Primates are the most colorful mammalian order and therefore serve as a critical group of mammals to examine the evolution of color diversity, yet primate hair coloration is understudied. We demonstrate that primate hair color diversity is the result of different evolutionary processes often acting independently across body regions. The torso and hind limbs follow a non-phylogenetic model of evolution and exhibit a high degree of evolutionary lability, which supports previous mammalian color studies arguing for the importance of a species' environment for shaping their coloration (Stoner et al. 2003; Kamilar and Bradley 2011b; Caro et al. 2017b). The head and forelimbs exhibit less evolutionary lability and have higher phylogenetic signals, which could be driven by their roles in signaling or communication (Santana et al. 2012; Allen et al. 2014; Martin et al. 2015). Hair color diversity also varies across primate clades: strepsirrhine coloration falls within a much smaller, lighter range of color compared to catarrhines and platyrrhines. This relationship between color diversity and clade may partially reflect the selective regimes of biological traits on coloration.

Visual system, activity pattern, and habitat shape the rate and optimal trait values of hair color evolution. Across body regions, nocturnal activity patterns, dichromatic and monochromatic vision, and drier habitats appear to shift hair color towards lighter pigmentation. Conversely, diurnal activity patterns, trichromatic vision, and wetter habitats are associated with more intermediate color values. Habitat appears to shape the rate of color evolution across body regions, and it is the only biological trait that seems to significantly shape torso coloration. Alongside existing studies on torso coloration in other mammalian orders, the evolution of torso coloration in terrestrial mammals repeatedly appears to be determined by ecological factors. The role of visual systems in shaping the evolutionary rate of head, forelimb, and tail coloration emphasizes the importance of conspecific perception and signaling in these body regions. Though there is less diversity in visual systems within other mammalian orders, future research examining the role of conspecific perception in guiding hair coloration may be fruitful in other mammalian clades that exhibit variation in activity patterns.

We note that our study focuses on primate hair coloration, and does not account for variation within primate skin coloration nor the selective pressures shaping this variation. Nonetheless, primate skin color is well studied compared to hair coloration, and our results provide new insights on broad patterns of hair color evolution across the extraordinarily colorful primate order.

Our results emphasize the importance of investigating patterns of trait evolution across regions of the body, as

well as incorporating relevant biological and ecological traits into evolutionary models. Future mammalian studies that are able to incorporate genetic data and other proximate mechanisms into explaining some of the macroevolutionary patterns we demonstrate here should yield exciting results.

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Author Contributions RBB and JMK conceived and designed the analysis. JMK collected the raw hair color data. RBB performed the statistical analyses and drafted the manuscript. RBB, JMK, and BJB interpreted the results and edited the manuscript.

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Data Availability Data are archived via the Dryad Digital Repository <https://doi.org/10.5061/dryad.dbrv15f16>.

Code Availability Code is archived via the Dryad Digital Repository <https://doi.org/10.5061/dryad.dbrv15f16>.

Declarations

Conflicts of Interest The authors declare no conflicts of interest.

References

- Allen WL, Moreno N, Gamble T, Chiari Y (2020) Ecological, behavioral, and phylogenetic influences on the evolution of dorsal color pattern in geckos. *Evolution* 74(6):1033–1047
- Allen WL, Stevens M, Higham JP (2014) Character displacement of Cercopithecini primate visual signals. *Nat Commun* 5:1–10
- Anderson TM, Candille SI, Musiani M, Greco C, Stahler DR, Smith DW, Padhukasahasram B, Randi E, Leonard JA, Bustamante CD, Ostrander EA, Tang H, Wayne RK, Barsh GS (2009) Molecular and evolutionary history of melanism in North American gray wolves. *Science* 323(5919):1339–1343
- Arnold C, Matthews J, Nunn CL (2010) The 10kTrees website: a new online resource for primate phylogeny. *Evol Anthropol* 19:114–118
- Baker J, Venditti C (2019) Rapid change in mammalian eye shape is explained by activity pattern. *Curr Biol* 29(6):1082–1088
- Bell RC, Webster GN, Whiting MJ (2017) Breeding biology and the evolution of dynamic sexual dichromatism in frogs. *J Evol Biol* 30(12):2104–2115

- Bergeron ZT, Fuller RC (2018) Using human vision to detect variation in avian coloration: how bad is it? *Am Nat* 191:269–276
- Bergman TJ, Ho L, Beehner JC (2009) Chest color and social status in male geladas (*Theropithecus gelada*). *Int J Primatol* 30(6):791–806
- Bradley BJ, Gerald MS, Widdig A, Mundy NI (2013) Coat color variation and pigmentation gene expression in rhesus macaques (*Macaca mulatta*). *J Mammal Evol* 20:263–270
- Bradley BJ, Mundy NI (2008) The primate palette: the evolution of primate coloration. *Evol Anthropol* 17:97–111
- Burnham KP, Anderson DR (2003) Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer Science and Business Media, Berlin
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* 65(1):23–35
- Butler MA, King AA (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am Nat* 164:683–695
- Caro T (2005) The adaptive significance of coloration in mammals. *BioScience* 55:125–136
- Caro T (2008) Contrasting coloration in terrestrial mammals. *Philos Trans R Soc B: Biol Sci* 364:537–548
- Caro T, Beeman K, Stankowich T, Whitehead H (2011) The functional significance of colouration in cetaceans. *Evol Ecol* 25(6):1231
- Caro T, Mallarino R (2020) Coloration in mammals. *Trends Ecol Evol* 35(4):357–366
- Caro T, Stankowich T, Mesnick SL, Costa DP, Beeman K (2012) Pelage coloration in pinnipeds: functional considerations. *Behav Ecol* 23(4):765–774
- Caro T, Walker H, Rossman Z, Hendrix M, Stankowich T (2017a) Why is the giant panda black and white? *Behav Ecol* 28(3):657–667
- Caro T, Walker H, Santana SE, Stankowich T (2017b) The evolution of anterior coloration in carnivorans. *Behav Ecol Sociobiol* 71(12):177
- Clavel J, Escarguel G, Merceron G (2015) mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol Evol* 6:1311–1319
- Clough D, Heistermann M, Kappeler PM (2009) Individual facial coloration in male *Eulemur fulvus rufus*: a condition-dependent ornament? *Int J Primatol* 30(6):859–875
- Cooper N, Thomas GH, Venditti C, Meade A, Freckleton RP (2016) A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biol J Linn Soc* 118:64–77
- Cramer JD, Gaetano T, Gray JP, Grobler P, Lorenz JG, Freimer NB, Schmitt CA, Turner TR (2013) Variation in scrotal color among widely distributed vervet monkey populations (*Chlorocebus aethiops pygerythrus* and *Chlorocebus aethiops sabaesus*). *Am J Primatol* 75(7):752–762
- Crouch NM, Ricklefs RE (2019) Speciation rate is independent of the rate of evolution of morphological size, shape, and absolute morphological specialization in a large clade of birds. *Am Nat* 193:E78–E91
- Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, Hill GE, Jablonski NG, Jiggins CD, Kelber A, Mappes J (2017) The biology of color. *Science* 357:eaan0221
- Darwin C (1859) On the Origin of Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life. John Murray, London
- delBarco-Trillo J, Burkert BA, Goodwin TE, Drea CM (2011) Night and day: the comparative study of strepsirrhine primates reveals socioecological and phylogenetic patterns in olfactory signals. *J Evol Biol* 24:82–98
- Dubuc C, Allen WL, Maestriperi D, Higham JP (2014) Is male rhesus macaque red color ornamentation attractive to females? *Behav Ecol Sociobiol* 68(7):1215–1224
- Dunn PO, Armenta JK, Whittingham LA (2015) Natural and sexual selection act on different axes of variation in avian plumage color. *Sci Adv* 1(2):e1400155
- Endler JA (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34(1):76–91
- Fernandez AA, Morris MR (2007) Sexual selection and trichromatic color vision in primates: statistical support for the preexisting-bias hypothesis. *Am Nat* 170(1):10–20
- Fleagle JG (2013) Primate Adaptation and Evolution. 3rd Ed. Academic Press, Cambridge
- Fleagle JG, Gilbert CC, Baden AL (2010) Primate cranial diversity. *Am J Phys Anthropol* 142:565–578
- Friedman NR, Remeš V (2015) Rapid evolution of elaborate male coloration is driven by visual system in Australian fairy-wrens (Maluridae). *J Evol Biol* 28(12):2125–2135
- Gloger CL (1833) Das Abändern der Vogel durch Einfluss des Klimas. August Schulz, Breslau
- Haitina T, Ringholm A, Kelly J, Mundy NI, Schiöth HB (2007) High diversity in functional properties of melanocortin 1 receptor (MC1R) in divergent primate species is more strongly associated with phylogeny than coat color. *Mol Biol Evol* 24:2001–2008
- Hall MI, Kamilar JM, Kirk EC (2012) Eye shape and the nocturnal bottleneck of mammals. *Proc R Soc B* 279:4962–4968
- Harmon LJ, Losos JB, Jonathan Davies T, Gillespie RG, Gittleman JL, Bryan Jennings W, Kozak KH, McPeck MA, Moreno-Roark F, Near TJ, Purvis A, Ricklefs RE, Schluter D, Schulte II JA, Seehausen O, Sidlauskas BL, Torres-Carvajal O, Weir JT, Mooers AØ (2010) Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64:2385–2396
- Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131
- Henzi SP (1985) Genital signalling and the coexistence of male vervet monkeys (*Cercopithecus aethiops pygerythrus*). *Folia Primatol* 45(3–4):129–147
- Hill GE, McGraw KJ (2006) Bird Coloration, Volume 1: Mechanisms and Measurements. Harvard University Press, Cambridge
- Hoekstra HE (2006) Genetics, development and evolution of adaptive pigmentation in vertebrates. *Heredity* 97:222–234
- Hoekstra HE, Drumm KE, Nachman MW (2004) Ecological genetics of adaptive color polymorphism in pocket mice: geographic variation in selected and neutral genes. *Evolution* 58(6):1329–1341
- Hoekstra HE, Nachman MW (2003) Different genes underlie adaptive melanism in different populations of rock pocket mice. *Mol Ecol* 12(5):1185–1194
- Hofreiter M, Schöneberg T (2010) The genetic and evolutionary basis of colour variation in vertebrates. *Cell Mol Life Sci* 67:2591–2603
- Jacobs GH (1993) The distribution and nature of colour vision among the mammals. *Biol Rev Biol Proc Camb Philos Soc* 68(3):413–471
- Jacobs RL, MacFie TS, Spriggs AN, Baden AL, Morelli TL, Irwin MT, Lawler RR, Pastorini J, Mayor M, Lei R, Culligan R, Hawkins MTR, Kappeler PM, Wright PC, Louis Jr EE, Mundy NI, Bradley BJ (2017) Novel opsin gene variation in large-bodied, diurnal lemurs. *Biol Lett* 13:20170050
- Jacobs RL, Veilleux CC, Louis EE, Herrera JP, Hiramatsu C, Frankel DC, Irwin MT, Melin AD, Bradley BJ (2019) Less is more: lemurs (*Eulemur* spp.) may benefit from loss of trichromatic vision. *Behav Ecol Sociobiol* 73(2):22
- Jones MR, Mills LS, Alves PC, Callahan CM, Alves JM, Lafferty DJ, Jiggins FM, Jensen JD, Melo-Ferreira J, Good JM (2018) Adaptive introgression underlies polymorphic seasonal camouflage in snowshoe hares. *Science* 360(6395):1355–1358

- Kamilar JM (2009) Interspecific variation in primate countershading: effects of activity pattern, body mass, and phylogeny. *Int J Primatol* 30(6):877
- Kamilar JM, Bradley BJ (2011a) Countershading is related to positional behavior in primates. *J Zool* 283:227–233
- Kamilar JM, Bradley BJ (2011b) Interspecific variation in primate coat colour supports Gloger's rule. *J Biogeogr* 38:2270–2277
- Kamilar JM, Cooper N (2013) Phylogenetic signal in primate behaviour, ecology and life history. *Philos Trans R Soc B: Biol Sci* 368:20120341
- Kamilar JM, Heesy CP, Bradley BJ (2013) Did trichromatic color vision and red hair color coevolve in primates? *Am J Primatol* 75:740–751
- Kamilar JM, Muldoon KM (2010) The climatic niche diversity of Malagasy primates: a phylogenetic perspective. *PLoS One* 5(6):e11073
- Kappeler PM (2012) The behavioral ecology of strepsirrhines and tarsiers. In: Mitani JC, Call P, Kappeler PM, Palombit RA, Silk JB (eds) *The Evolution of Primate Societies*. University of Chicago Press, Chicago, pp 17–42
- Kawamura S (2016) Color vision diversity and significance in primates inferred from genetic and field studies. *GENES GENOM* 38:779–791
- Kawamura S, Kubotera N (2004) Ancestral loss of short wave-sensitive cone visual pigment in lorisiform prosimians, contrasting with its strict conservation in other prosimians. *J Mol Evol* 58(3):314–321
- Luzuriaga-Aveiga VE, Weir JT (2019) Elevational differentiation accelerates trait evolution but not speciation rates in Amazonian birds. *Ecol Lett* 22(4):624–633
- Maddison WP, Maddison DR (2017) Mesquite: a modular system for evolutionary analysis. Version 3.31. URL: <http://www.mesquiteproject.org>
- Maia R, Rubenstein DR, Shawkey MD (2013) Key ornamental innovations facilitate diversification in an avian radiation. *Proc Natl Acad Sci USA* 110(26):10687–10692
- Manceau M, Domingues VS, Linnen CR, Rosenblum EB, Hoekstra HE (2010) Convergence in pigmentation at multiple levels: mutations, genes and function. *Philos Trans R Soc B: Biol Sci* 365:2439–2450
- Marcondes RS, Brumfield RT (2019) Fifty shades of brown: macroevolution of plumage brightness in the furnariida, a large clade of drab neotropical passerines. *Evolution* 73:704–719
- Martin PR, Montgomerie R, Loughheed SC (2015) Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *Am Nat* 185:443–451
- McGarigal K, Stafford S, Cushman S (2000) *Multivariate Statistics for Wildlife and Ecology Research*. Springer, New York
- McNaught MK, Owens IPF (2002) Interspecific variation in plumage coloration among birds: species recognition or light environment? *J Evol Biol* 15:505–514
- Mundy NI, Kelly J (2003) Evolution of a pigmentation gene, the melanocortin-1 receptor, in primates. *Am J Phys Anthropol* 121(1):67–80
- Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffrers K, Thuiller W (2012) How to measure and test phylogenetic signal. *Methods Ecol Evol* 3:743–756
- Nilsson Sköld H, Aspöngren S, Wallin M (2013) Rapid color change in fish and amphibians—function, regulation, and emerging applications. *Pigment Cell Melanoma Res* 26(1):29–38
- O'Meara BC, Ané C, Sanderson MJ, Wainwright PC (2006) Testing for different rates of continuous trait evolution using likelihood. *Evolution* 60:922–933
- Ortolani A (1999) Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biol J Linn Soc* 67:433–476
- Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401:877–884
- Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35(3):526–528
- Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, FitzJohn RG, Alfaro ME, Harmon LJ (2014) geiger v2. 0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30(15):2216–2218
- Petersdorf M, Dubuc C, Georgiev AV, Winters S, Higham JP (2017) Is male rhesus macaque facial coloration under intrasexual selection? *Behav Ecol* 28(6):1472–1481
- Price TD (2017) Sensory drive, color, and color vision. *Am Nat* 190:157–170
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rakotonirina H, Kappeler PM, Fichtel C (2017) Evolution of facial color pattern complexity in lemurs. *Sci Rep* 7:1–18
- Renoult JP, Schaefer HM, Sallé B, Charpentier MJ (2011) The evolution of the multicoloured face of mandrills: insights from the perceptual space of colour vision. *PLoS One* 6(12): e29117
- Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* 3:217–223
- Ribot RF, Berg ML, Schubert E, Endler JA, Bennett AT (2019) Plumage coloration follows Gloger's rule in a ring species. *J Biogeogr* 46(3):584–596
- Romero-Díaz C, Rivera JA, Ossip-Draho AG, Zúñiga-Vega JJ, Vital-García C, Hews DK, Martins EP (2019) Losing the trait without losing the signal: evolutionary shifts in communicative colour signalling. *J Evol Biol* 32(4):320–330
- Rowe N, Myers M (2017) All the World's Primates. Primate Conservation Inc. <http://alltheworldsprimates.org>
- Rowan J, Beaudrot L, Franklin J, Reed KE, Smail IE, Zamora A, Kamilar JM (2020) Geographically divergent evolutionary and ecological legacies shape mammal biodiversity in the global tropics and subtropics. *Proc Natl Acad Sci USA* 117(3):1559–1565
- Rowan J, Kamilar JM, Beaudrot L, Reed KE (2016) Strong influence of palaeoclimate on the structure of modern African mammal communities. *Proc R Soc B* 283(1840):20161207
- Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. *Oxford Surv Evol Biol* 7:157–195
- Santana SE, Alfaro JL, Alfaro ME (2012) Adaptive evolution of facial colour patterns in Neotropical primates. *Proc R Soc B* 279:2204–2211
- Santana SE, Alfaro JL, Noonan A, Alfaro ME (2013) Adaptive response to sociality and ecology drives the diversification of facial colour patterns in catarrhines. *Nat Commun* 4(1):1–7
- Schaefer HM, Schaefer V, Levey DJ (2004) How plant–animal interactions signal new insights in communication. *Trends Ecol Evol* 19:577–584
- Schliep KP (2011) phangorn: phylogenetic analysis in R. *Bioinformatics* 27:592–593
- Seehausen O, Mayhew PJ, Van Alphen JJM (1999) Evolution of colour patterns in East African cichlid fish. *J Evol Biol* 12:514–534
- Setchell JM (2005) Do female mandrills prefer brightly colored males? *Int J Primatol* 26(4):715–735
- Setchell JM, Jean Wickings E, Knapp LA (2006) Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proc R Soc B* 273(1599):2395–2400
- Sheets AD, Chavez AS (2020) Evolution of pelage luminance in squirrels (Sciuridae). *Front Ecol Evol* 8:249
- Soul LC, Friedman M (2015) Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses. *Syst Biol* 64:608–620

- Stevens M, Parraga CA, Cuthill IC, Partridge JC, Troscianko TS (2007) Using digital photography to study animal coloration. *Biol J Linn Soc* 90:211–237
- Stoddard MC, Prum RO (2008) Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *Am Nat* 171:755–776
- Stoddard MC, Prum RO (2011) How colorful are birds? Evolution of the avian plumage color gamut. *Behav Ecol* 22:1042–1052
- Stoner CJ, Caro TM, Graham CM (2003) Ecological and behavioral correlates of coloration in artiodactyls: systematic analyses of conventional hypotheses. *Behav Ecol* 14(6): 823–840
- Sumner P, Mollon JD (2003) Colors of primate pelage and skin: objective assessment of conspicuousness. *Am J Primatol* 59:67–91
- Tan Y, Li WH (1999) Trichromatic vision in prosimians. *Nature* 402(6757):36
- Tapanes E, Kamilar JM, Bradley BJ (In press) Molecular and cellular processes of pelage pigmentation and growth in primate evolution. In: Pitirri MK, Richtsmeier JT (eds) *Evolutionary Cell Processes in Primates: Genes, Skin, Energetics, Breathing, and Feeding, Volume II*. Taylor and Francis/CRC Press, New York
- Valenta K, Edwards M, Rafaliarison RR, Johnson SE, Holmes SM, Brown KA, Dominy NJ, Lehman SM, Parra EJ, Melin AD (2016) Visual ecology of true lemurs suggests a cathemeral origin for the primate cone opsin polymorphism. *Funct Ecol* 30:932–942
- Veilleux CC, Jacobs RL, Cummings ME, Louis EE, Bolnick DA (2014) Opsin genes and visual ecology in a nocturnal folivorous lemur. *Int J Primatol* 35(1):88–107
- Waite C, Little AC, Wolfensohn S, Honess P, Brown AP, Buchanan-Smith HM, Perrett DI (2003) Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proc R Soc B* 270(suppl_2):S144-S146
- Wallace AR (1870) *Contributions to the Theory of Natural Selection: A Series of Essays*. Macmillan and Company, London
- Wang JJ, Shaffer HB (2008) Rapid color evolution in an aposematic species: a phylogenetic analysis of color variation in the strikingly polymorphic strawberry poison-dart frog. *Evolution* 62(11):2742–2759
- West PM, Packer C (2002) Sexual selection, temperature, and the lion's mane. *Science* 297:1339–1343
- Wickham H (2009) *ggplot2: Elegant Graphic for Data Analysis*. Springer, New York

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