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RESEARCH ARTICLE

Did Trichromatic Color Vision and Red Hair Color Coevolve in Primates?

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Reddish pelage and red hair ornaments have evolved many times, independently, during primate evolution. It is generally assumed that these red-coat phenotypes, like red skin phenotypes, play a role in sociosexual signaling and, thus evolved in tandem with conspecific color vision. This study examines the phylogenetic distribution of color vision and pelage coloration across the primate order to ask: (1) did red pelage and trichromacy coevolve; or (2) did trichromacy evolve first, and then subsequently red pelage evolved as an exaptation? We collected quantitative, color-corrected photographic color data for 142 museum research skins from 92 species representing 41 genera spanning all major primate lineages. For each species, we quantified the ratio of Red/Green values (from a RGB color model) at 20 anatomical landmarks. For these same species, we compiled data on color vision type (routine trichromatic, polymorphic, routine dichromatic, monochromatic) and data on variables that potentially covary with visual system (VS) and coloration, including activity pattern and body mass dimorphism (proxy for sexual selection). We also considered whether the long-term storage of research skins might influence coloration. Therefore, we included the time since the specimen was collected as an additional predictor. Analyzing the data with phylogenetic generalized least squares models, we found that the amount of red hair present in primates is associated with differences in VSs, but not in the direction expected. Surprisingly, trichromatic primate species generally exhibited less red hair compared to red-green colorblind species. Thus, our results do not support the general assumption that color vision and red pelage coloration are a coevolutionary product of sociosexual signaling in primates. In addition, we did not find an effect of activity pattern, body mass dimorphism, or time since collection on the redness of primate hair. Our results have important implications for the evolution of primate coloration and visual systems. Am. J. Primatol. 75:740–751, 2013.

Key words: pigmentation; coloration; pelage; coat color; camouflage; opsin

INTRODUCTION

Primates have evolved a unique combination of visual specializations that differentiate them from other mammals [Heesy, 2008, 2009; Kaas, 2013; Preuss, 2007; Ross & Martin, 2007]. Among these specializations is the presence of polymorphic or routine trichromatic color vision found in several primate lineages [Jacobs, 1993, 1994/1995; Jacobs, 2009; see Fig. S2]. Catarrhines possess routine trichromacy, which imparts the ability to distinguish between the green to the longer wavelength red portion of the visual spectrum in both males and females [Jacobs, 1994/1995]. Many platyrrhines and several species of lemuriforms have also evolved an x-linked polymorphism at the middle/long wavelength (i.e., green-red) sensitive opsin allele which, in heterozygous females, imparts functional trichromacy [e.g., Jacobs, 1994/1995; Jacobs, 2009; Kawamura et al., 2012; Veilleux & Bolnick, 2009]. Thus, in these polymorphic species there is individual variation in the potential for color discrimination among heterozygous females, which express complementary shorter (green sensitive) and somewhat longer (orange-red sensitive) alleles, and males and homozygous females, which do not.

Phylogenetic analyses of the distribution of opsin genes among primates support the hypothesis that

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both polymorphic color vision and routine trichromacy have evolved independently multiple times via either allelic differentiation or gene duplication [Heesy & Ross, 2001, 2004; Kawamura et al., 2012; Surridge et al., 2003; but see Tan et al., 2005]. Adaptive explanations for primate trichromacy have concentrated on the potential foraging advantages that an additional red color channel could provide; namely the ability to detect either ripe red fruits or, alternatively, young red leaves against a dappled green background [Dominy & Lucas, 2001; Dominy et al., 2003; Regan et al., 2001]. Although the available data support the visual targeting of young red leaves (at least by larger sized anthropoids), the relatively weak relationship between photoreceptor responses in catarrhines and the spectra of dietary items suggests that the selective influences are either not strongly tied to any particular diet [Osorio & Vorobyev, 1996], or additional natural spectra are relevant to the catarrhine visual palette. In addition, relevant natural targets in the environment potentially include landmarks for navigation, predators, or conspecifics. There is strong evidence that animal coloration is related to the latter two possibilities as skin and coat pigmentation can serve as potential background matching to avoid detection by predators, or as signaling to potential mates and other conspecifics [Bradley & Mundy, 2008; Kamilar, 2009; Kamilar & Bradley, 2011a; Merilaita & Stevens, 2011; Rowland, 2011; Ruxton et al., 2004; Troscianko et al., 2009].

The color red, in particular, often plays an important role in conspecific signaling [Hill & Barton, 2005; Setchell et al., 2006; Waitt et al., 2003]. In birds, red-hued feathers can provide an honest cue of health and nutritional status [Hill & Montgomerie, 1994] as red bird coloration is often [though not always, see McGraw, 2004] obtained through carotenoids in the diet [Griffith et al., 2006]. In contrast to birds, ingested carotenoids are not readily incorporated into mammalian skin or hair [Bradley & Mundy, 2008; but see Stephen et al., 2011]. Mammals, especially primates, show striking examples of red signaling, most notably through red skin ornaments on the face [Setchell et al., 2006], chest [Bergman et al., 2009] or anogenital region [Higham et al., 2012; Nunn, 1999; Pagel, 1994]. Red in this case is due to hemoglobin in oxygen-saturated blood in the superficial layers of the skin. In fact, Changizi et al. [2006] argue that trichromatic primates are particularly sensitive to variations in skin color due to blood oxygen saturation (i.e., "blushing"), suggesting an important relationship between conspecific red signaling and color vision during primate evolution.

Many primates also exhibit bright red pelage or red hair ornaments [Bradley & Mundy, 2008; Santana et al., 2012]. Indeed, the independent, convergent evolution of red hair has occurred repeatedly in primate evolution, including during recent human evolution; genetic analysis of pigmentation genes (*MC1R*) indicate that at least some Neanderthals had red hair, though the genetic mechanism differs from that of modern human red-heads [Lalueza-Fox et al., 2007].

The reddish or auburn coats of many primates, such as red ruffed lemurs, golden-lion tamarins and orangutans, are an anomaly among the normally dark, drab pelage phenotype of most mammals [Caro, 2005]. As with red sexual skin, it is assumed that such red hair signals are related to the evolution of trichromacy in primates, though this has not been well quantified or demonstrated. Fernandez and Morris [2007] provide the only comparative study examining the timing and phylogenetic distribution of red hair across primates, and their results suggest that red pelage and red skin evolved along primate lineages following the emergence of trichromatic color vision. However, more recent evidence suggests that their study was limited in several ways, including the incorrect scoring of color vision phenotype for many strepsirrhine species (all were assumed to be mono- or dichromatic), a lack of quantitative data on pelage and skin color (presence–absence red scoring was based only on descriptions in field guides), and an outdated primate phylogeny [Purvis, 1995], which call their results into question [Bradley & Mundy, 2008].

Here, we provide a quantitative, comparative analysis of color vision and pelage coloration across the primate order. We also include data on variables that may covary with visual system (VS) and pelage variables: activity pattern (a correlate of ecologically relevant light levels) and body mass dimorphism (a surrogate for sexual selection). Here we test two complementary hypotheses: (1) trichromacy and red pelage coevolved in multiple primate lineages; and (2) trichromacy served as an exaptation for the subsequent evolution of red pelage in multiple primate lineages. Both hypotheses assume that trichromacy and red pelage function for sociosexual signaling.

METHODS

This research adhered to all legal requirements of the United States, and complied with IACUC protocols from Midwestern and Yale University. It also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Data Collection

We collected hair color data from 142 female museum research skins, representing 92 species and 41 genera from all major primate lineages (Figs. S1 and S2). All museum research skins were housed at the American Museum of Natural History and the Field

TABLE I. Sampling Locations where Color Was Quantified for Each Museum Skin

Location	Definition
Mid cap	Midway between ears and midway between superior margin of eye and inferior most part of head
Outer crown	Medial ear margin
Upper back	Mediolateral midpoint of back, where the forelimbs meet the torso
Mid back	Mediolateral midpoint of back, at the midpoint between the superior and inferior edges of the back
Dorsal upper forelimb	Midpoint of upper forelimb; dorsal side
Dorsal lower forelimb	Midpoint of lower forelimb; dorsal side
Dorsal hand	Dorsal side of hand
Dorsal upper hindlimb	Midpoint of upper hindlimb; dorsal side
Dorsal lower hindlimb	Midpoint of lower hindlimb; dorsal side
Dorsal foot	Dorsal side of foot
Dorsal proximal tail[a]	Proximal most part of the tail
Dorsal distal tail	Distal most part of the tail; dorsal side
Ventral neck	Center section of the ventral neck
Ventral upper forelimb	Midpoint of upper forelimb; ventral side
Ventral lower forelimb	Midpoint of lower forelimb; ventral side
Upper chest	Analogous point to the upper back on the ventral surface of the torso
Middle chest	Analogous point to the mid back on the ventral surface of the torso
Ventral upper hindlimb	Midpoint of upper hindlimb; ventral side
Ventral lower hindlimb	Midpoint of lower hindlimb; ventral side
Ventral distal tail	Distal most part of the tail; ventral side

[a]For species with no tail or highly reduced tail, color was sampled at the coccyx region. The same color values were used for proximal and distal locations, including the distal ventral location.

Museum of Natural History. We only used research skins that were in good condition at the majority of sampling locations (more details below) and were not on public display. We employed a digital photographic approach that has been successfully used in prior research to obtain objective color measurements [Gerald et al., 2001; Kamilar, 2009; Kamilar & Bradley, 2011a, 2011b; Stevens et al., 2007]. This is important because differences in lighting conditions, camera settings, and background color can influence the apparent color of an object [Stevens et al., 2007, 2009]. Briefly, an X-rite Colorchecker chart was placed in the frame with each museum skin when it was photographed. We used a Canon Rebel XTI digital camera to obtain photographs of each specimen and then color calibrated the images using the Pictocolor plug-in for Adobe Photoshop, which contained the known color values present in the Colorchecker chart. Further details of the camera settings and color calibration procedure can be found in our recent publications [Kamilar, 2009; Kamilar & Bradley, 2011a, 2011b].

Several color models can be used to represent the color of digital photographs [Montgomerie, 2006]. Since the main goal of our study was to measure the amount of red hair exhibited by primates, we chose the RGB color model for our color sampling. We measured "red" in two ways: (1) the mean Red/Green channel ratio across all sampling locations per museum skin and (2) the maximum Red/Green channel ratio across all sampling locations per museum skin. Higher values indicate more "redness." We considered other metrics to define "red," such as (Red − Green)/(Red + Green), yet our results using this approach did not differ in their qualitative significance. It is important to note that the long and medium wavelength sensors of digital cameras are spaced further apart that the equivalent receptors of trichromatic primates [Higham et al., 2010]. Therefore, using a camera may exaggerate the difference between Red and Green signals when compared to what is perceived by trichromats.

We quantified color at 20 sampling locations for each museum skin (Table I). Although not exhaustive, these sampling locations often vary in color across species based on our experience examining several hundred museum specimens [Kamilar, 2009; Kamilar & Bradley, 2011a, 2011b]. We were able to obtain data from more than one research skin for several species (Figs. S1 and S2). In these cases, we used the average value at each sampling location to represent the species-level data point. For 12 specimens, reliable color measurements were not possible at all locations (e.g., each species was missing one sampling location). Therefore, the missing sampling locations were not included in our mean or maximum Red/Green calculations for these species.

Our method of quantifying primate hair color is likely not applicable to measuring the coloration of other tissue types. For instance, the bluish or purplish skin of mandrills, guenons, or vervet monkeys [e.g., Gerald, 2001] would not be accurately quantified by using the Red and Green channels alone. In these cases, explicitly accounting for variation in the Blue channel would be critical. In contrast, primate hair occupies a relatively small portion of the

possible color space, primarily varying along two axes. The first is related to variation in luminance, with little chromatic variation (i.e., similar Red, Green, and Blue values indicating hair that is either white, a shade of gray, or black). The other is along a red/brown axis, where the Green and Blue channels are similar, and the Red channel exhibits higher values. Hair appears increasingly red as the ratio of Red to Green-Blue increases. To confirm the tight correlation between the Green and Blue channels, we conducted Pearson's correlations using the Blue and Green values at each anatomical landmark we sampled. The correlation coefficient was at least $r = 0.93$ in all cases.

In addition to quantifying the hair color of each specimen, we also included three additional predictor variables that may influence the relationship between VSs and hair color. We recorded the year the specimen was collected from the field. The information was used to calculate the time (in years) between the collection date and the date of the photograph. Although there has been no quantitative examination of the effect of time on museum skin quality, prior research using bird specimens showed that some species became darker with age [Armenta et al., 2008]. In addition, museum staff members (e.g., Stanley, personal communication) have noted that museum pelages may become redder with time (i.e., "foxing"), but this is known to occur when specimens are on public display, being exposed to ambient light for many years. Though, in a recent paper, we added time as a covariate in a generalized linear model and found no effect of time on the brightness of primate hair [Kamilar & Bradley, 2011b].

We also gathered data for the activity pattern and body mass dimorphism of each species. The activity pattern of each species was quantified as either diurnal, cathemeral, or nocturnal. Activity pattern data were obtained from Campbell and colleagues [2007] and Fleagle [1999]. Body mass dimorphism was calculated as ratio of male mass/female mass. Sex-specific body mass data were obtained from Isler et al. [2008] and Smith and Jungers [1997].

Finally, we categorized the VS of each sex for each species. Using sex-specific VSs was necessary because numerous species (especially noncatarhines) exhibit sex differences in their color VS [Bradley & Mundy, 2008; Surridge et al., 2003]. We quantified four types of VSs for females: (1) monochromatic, (2) dichromatic, (3) polymorphic dichromatic-trichromatic, (4) trichromatic. We quantified three types of VSs for males: (1) monochromatic, (2) dichromatic, (3) trichromatic. VS data were obtained from several sources in the literature [Bradley & Mundy, 2008; Surridge et al., 2003; Fig. S1]. Five species have unknown female VSs (*Avahi laniger*, *Eulemur albocollaris*, *E. coronatus*, *E. fulvus*, *E. sanfordi*), therefore, they were not included in the female VS analyses.

Data Analysis

We conducted phylogenetic generalized least squares models (PGLS) with Pagel's lambda [Freckleton et al., 2002; Pagel, 1999] to analyze our data. Phylogenetic comparative methods were necessary because of the interspecific nature of our data set. Related species are often biologically similar, resulting in potentially nonindependent samples being used in statistical analyses [Felsenstein, 1985; Nunn, 2011]. Phylogenetic comparative methods quantitatively account for the evolutionary relationships among species, alleviating the problem of statistical nonindependence. PGLS with lambda has become an increasingly popular method in comparative biology [e.g., Heesy et al., 2011; Kamilar & Bradley, 2011b; Pointer et al., 2012]. This method is an improvement over older methods, such as phylogenetically independent contrasts [Felsenstein, 1985], because the error structure of the model is not assumed to perfectly follow a Brownian motion model of evolution. Lambda varies continuously from zero to one, with zero indicating that the residuals of the model are not correlated to phylogeny. In other words, a zero lambda value is equivalent to a nonphylogenetic model. If lambda is one, then the residuals of the model perfectly follow a Brownian motion model, which is equivalent to an analysis using phylogenetically independent contrasts. Lambda was optimized using a maximum likelihood approach.

No recently published phylogeny contained all of the species in our data set. Therefore, we used the typology and branch lengths from a consensus tree obtained from the 10K Trees website [Arnold et al., 2010] for 87 of the 92 species in our data set. We used additional sources to add the remaining five species to our tree in the following manner. We treated *Aotus miconax* as monophyletic with the other *Aotus* species [Groves, 2001], and created a polytomy with the basal species of this genus. Similarly, we treated all *Pithecia* as a monophyletic group [Groves, 2001] and created a polytomy including *Pithecia monachus* and the two other *Pithecia* species from the 10K Trees phylogeny. Our data set included five *Callicebus* taxa, with *Callicebus cupreus* absent from the 10K Tree phylogeny. *C. cupreus* is a sister taxon to *C. moloch* per Perelman et al. [2011], yet this phylogeny does not contain *C. hoffmannsi*, which is in our data set. Therefore, we created a polytomy including *C. cupreus*, *C. moloch*, and *C. hoffmansi*. Finally, two *Presbytis* species, *P. comata* and *P. potenziani*, was also missing from the 10K Trees phylogeny. We followed Perelman et al. [2011] and set *P. comata* as the sister taxon to *P. melaphos*. In addition, we followed Meijaard and Groves [2004] and included *P. potenziani* as the basal *Presbytis* lineage. We set the divergence time for this species as the midpoint between the remaining two *Presbytis* species and the *Trachypithecus* clade (see Fig. S2 for phylogeny).

Although this approach is very rudimentary, error in the divergence time of this single species should have negligible effect on our results.

We performed four analyses for each of our four data sets (e.g., two methods to quantify VS × two methods to quantify red hair). Each analysis contained a different combination of predictor variables, with VS type and time since collection (T) used in all analyses. The four models included the following predictor variables—model 1: VS + T + activity pattern + body mass dimorphism; model 2: VS + T + body mass dimorphism; model 3: VS + T + activity pattern; model 4: VS + T. We treated VS as a categorical predictor (with four factors for females and three factors for males). Time since collection, body mass dimorphism, and activity pattern (ordered from the highest to lowest light levels while active: diurnal assigned a value of 1, cathemeral assigned a value of 2, and nocturnal assigned a value of 3) were defined as continuous predictors. We conducted another set of analyses treating activity pattern as a categorical predictor and obtained nearly identical results. We only present the results using the former approach here.

We used Akaike's information criterion with correction (AICc) for small sample size to judge the best models for each data set [Burnham & Anderson, 2002]. Basically, AICc uses a likelihood approach to rank models based on their explained variance relative to their complexity (i.e., number of model parameters). The model with the lowest AICc value is deemed the model that best explains the data. Models within 2 AICc values of the "best" model are considered equally good. This method of model selection is becoming increasingly common in comparative biology and biological anthropology [Kamilar et al., 2010; Tecot et al., 2012; Wheeler et al., 2011] and has several advantages over stepwise procedures [Burnham & Anderson, 2002; Hegyi & Garamszegi, 2011].

Red/Green ratios, time since collection, and body mass dimorphism were log-transformed prior to analysis to better meet the assumptions of parametric statistical tests [Quinn & Keough, 2002]. All PGLS analyses were conducted using the caper package (Orme et al., 2012; http://cran.r-project.org/web/packages/caper/index.html) in the R computing environment (R Development Core Team, 2011; http://cran.r-project.org/index.html). All analyses were two-tailed and we consider $P \leq 0.05$ to be statistically significant.

RESULTS

We found a significant difference in the amount of red hair present in primates with different VSs, yet not in the direction expected. Trichromatic primate species usually exhibited less red hair compared to species that lack cones that are not sensitive to wavelengths in the red portion of the visual spectrum (Tables II–III; Figs. 1–4). One way this is illustrated is by the proportion of primates in each VS category (based on female VSs) that exhibit mean Red/Green ratio values >1.2 (i.e., red channel was 20% higher than green). These "reddest" primates include 2.9% of trichromatic species (1 of 34: *Macaca nemestrina*), 22.9% of polymorphic species (8 of 35: three *Callicebus* species, two *Eulemur species*, *Leontopithecus rosalia*, *Saimiri oerstedii*, *Ateles geoffroyi*), 15.4% of dichromatic species (2 of 13: *Microcebus rufus*, *Cheirogaleus medius*), and 14.3% of monochromatic species (1 of 7: *Aotus lemurinus*; Figs. S1–S2).

When we categorized species by female VS and used the maximum Red/Green ratio, we found three equivalently good models based on AICc (Table II; Figs. 1–2 All three models exhibited P values at the 0.001 level or lower (model 2: PGLS, model $r^2 = 0.202$, full-model P value = 0.001, $n = 87$; model 3: PGLS, model $r^2 = 0.202$, full-model P value = 0.001, $n = 87$; model 4: PGLS, model $r^2 = 0.198$, full-model P value <0.001, $n = 87$). Monochromatic species exhibited significantly redder hair than trichromatic species in two of the three models. Dichromatic species exhibited significantly redder hair compared to trichromatic species in model 2 (PGLS, estimate = 0.074, $P = 0.05$, $n = 87$). Polymorphic species were significantly redder than trichromatic species in all three models (Table II). Pagel's lambda was zero in all models using this data set.

There were fewer differences among species with different VSs when we used the mean Red/Green ratio. This data set produced two equivalently good models based on AICc, yet both of these models did not reach statistical significance (model 3: PGLS, model $r^2 = 0.114$, $P = 0.06$, df = 87; model 4: PGLS, model $r^2 = 0.074$, $P = 0.07$, df = 87). We found that monochromatic species exhibited significantly redder hair than trichromatic species (PGLS, Estimate = 0.084, $P < 0.05$, $n = 87$) in model 2, though the full model P value was 0.14 (PGLS, model $r^2 = 0.093$, $n = 87$). Species with polymorphic female VSs displayed redder hair than trichromatic species, yet this difference was not statistically significant (PGLS, Estimate = 0.052, $P = 0.10$, $n = 87$) in model 4. Pagel's lambda ranged from 0.519 to 0.561 in these models.

We found even greater differences in the degree of red hair exhibited by primates with different male VSs. Based on the maximum Red/Green ratio values, we found three models that were equally good (Table III; Figs. 3–4). All three models exhibited P values <0.001 (model 2: PGLS, model $r^2 = 0.184$, full model P value <0.001, $n = 92$; model 3: PGLS, model $r^2 = 0.186$, full model P value < 0.001, $n = 92$; model 4: PGLS, model $r^2 = 0.182$, full model P value <0.001, $n = 92$). In addition, both monochromatic and dichromatic species were

TABLE II. Phylogenetic Generalized Linear Model Examining the Relationship between Female Visual System and the Amount of Red Hair in Primates

		Female visual system													
		Trichromatic		Monochromatic			Dichromatic			Polymorphic					
Measure of red hair	Model	Estimate	Standard error	Estimate	Standard error	*P* value	Estimate	Standard error	*P* value	Estimate	Standard error	*P* value	Model r^2	Model *P* value	Model AICc	Pagel's lambda
Red/Green ratio mean	1	0.207	0.103	0.017	0.065	0.79	0.003	0.058	0.97	0.046	0.033	0.17	0.114	0.12	−233.78	0.561
	2	0.249	0.107	**0.086**	**0.043**	**0.05**	0.056	0.043	0.19	0.053	0.032	0.10	0.093	0.14	−234.06	0.519
	3	0.208	0.101	0.017	0.064	0.79	0.002	0.057	0.97	0.045	0.032	0.16	**0.114**	**0.06**	**−236.15**	**0.561**
	4	0.255	0.096	0.085	0.041	0.18	0.056	0.041	0.18	0.052	0.031	0.10	**0.093**	**0.07**	**−236.40**	**0.521**
Red/Green ratio max	1	0.228	0.170	0.111	0.088	0.21	0.038	0.085	0.65	**0.108**	**0.031**	**0.001**	0.204	**<0.01**	−128.99	0.000
	2	0.212	0.178	**0.154**	**0.050**	**<0.01**	**0.083**	**0.041**	**0.05**	**0.113**	**0.031**	**<0.001**	**0.202**	**0.001**	**−131.13**	**0.000**
	3	0.231	0.169	0.102	0.085	0.24	0.032	0.083	0.70	**0.101**	**0.027**	**<0.001**	**0.202**	**0.001**	**−131.13**	**0.000**
	4	0.249	0.166	**0.143**	**0.046**	**<0.01**	**0.074**	**0.038**	**0.05**	**0.104**	**0.026**	**<0.001**	**0.198**	**<0.001**	**−133.10**	**0.000**

All analyses include 87 species.
Female visual system (VS) was used as a categorical predictor variable and time since collection (T) was used as a covariate in all models
Models included the following predictor variables—model 1: VS + T + activity pattern + body mass dimorphism; model 2: VS + T + body mass dimorphism; model 3: VS + T + activity pattern; model 4: VS + T.
P values associated with specific VSs are related to comparing differences between that particular VS versus trichromatic species. Positive Estimate values for nontrichromatic species indicate that these species exhibit redder hair compared to trichromatic species.
Activity pattern and body mass dimorphism was not statistically significant in any model.
Lower AICc values indicate a better model. Models within 2 AICc values of the lowest score are considered equivalently good. AICc values are not comparable across different data sets.
Bold fonts indicate statistically significant *P* values for specific predictors and the best full models according to AICc.

TABLE III. Phylogenetic Generalized Linear Model Examining the Relationship between Male Visual System and the Amount of Red Hair in Primates

		Male visual system											
		Trichromatic		Monochromatic			Dichromatic						
Measure of red hair	Model	Estimate	Standard error	Estimate	Standard error	*P* value	Estimate	Standard error	*P* value	Model r^2	Model *P* value	Model AICc	Pagel's lambda
Red/Green ratio mean	1	0.215	0.099	0.055	0.051	0.28	0.044	0.031	0.16	0.096	0.10	−250.81	0.486
	2	0.244	0.092	**0.082**	**0.040**	**0.04**	0.049	0.029	0.10	0.087	0.08	−252.15	0.448
	3	0.215	0.097	0.054	0.049	0.27	0.044	0.030	0.14	**0.096**	**0.05**	**−253.10**	**0.487**
	4	0.244	0.092	**0.082**	**0.038**	**0.03**	0.049	0.028	0.08	**0.087**	**0.03**	**−254.39**	**0.448**
Red/Green ratio max	1	0.257	0.164	**0.169**	**0.058**	**<0.01**	**0.105**	**0.030**	**0.001**	0.187	0.001	−142.07	0.000
	2	0.238	0.160	**0.153**	**0.049**	**<0.01**	**0.099**	**0.028**	**0.001**	**0.184**	**<0.001**	**−144.03**	**0.000**
	3	0.260	0.163	**0.162**	**0.055**	**<0.01**	**0.098**	**0.026**	**<0.001**	**0.186**	**<0.001**	**−144.16**	**0.000**
	4	0.240	0.159	**0.143**	**0.044**	**<0.01**	**0.091**	**0.024**	**<0.001**	**0.182**	**<0.001**	**−146.01**	**0.000**

All analyses include 92 species.
Male visual system (VS) was used as a categorical predictor variable and time since collection (T) was used as a covariate in all models
Models included the following predictor variables—model 1: VS + T + activity pattern + body mass dimorphism; model 2: VS + T + body mass dimorphism; model 3: VS + T + activity pattern; model 4: VS + T.
P values associated with specific VSs are related to comparing differences between that particular VS versus trichromatic species. Positive estimate values for nontrichromatic species indicate that these species exhibit redder hair compared to trichromatic species.
Activity pattern and body mass dimorphism was not statistically significant in any model.
Lower AICc values indicate a better model. Models within 2 AICc values of the lowest score are considered equivalently good. AICc values are not comparable across different data sets.
Bold fonts indicate statistically significant *P* values for specific predictors and the best full models according to AICc.

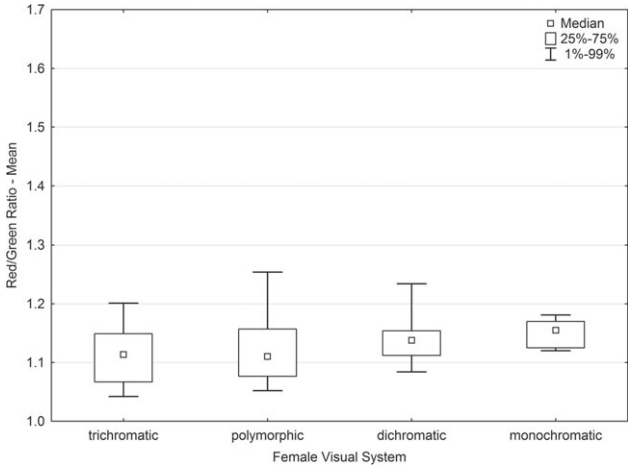

Fig. 1. Variation in the presence of red hair for primate species categorized by female visual systems. The redness of hair is quantified by the mean Red/Green ratio across all sampling locations on the pelage. Higher values indicate redder hair.

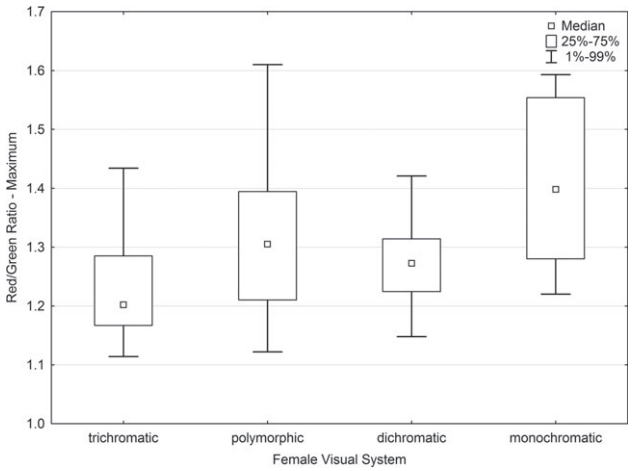

Fig. 2. Variation in the presence of red hair for primate species categorized by female visual systems. The redness of hair is quantified by the maximum Red/Green ratio sampled at any location on the pelage. Higher values indicate redder hair.

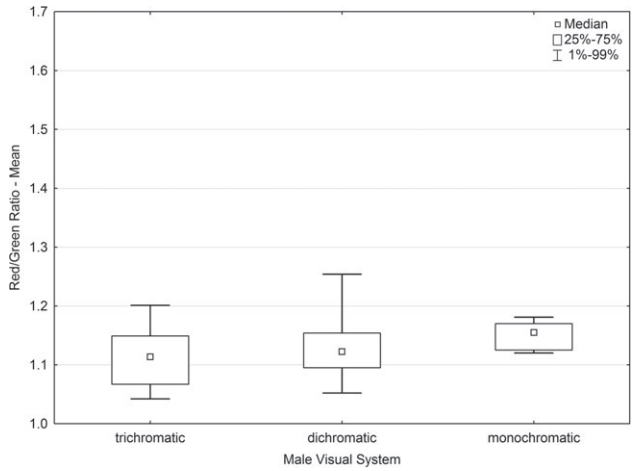

Fig. 3. Variation in the presence of red hair for primate species categorized by male visual systems. The redness of hair is quantified by the mean Red/Green ratio across all sampling locations on the pelage.

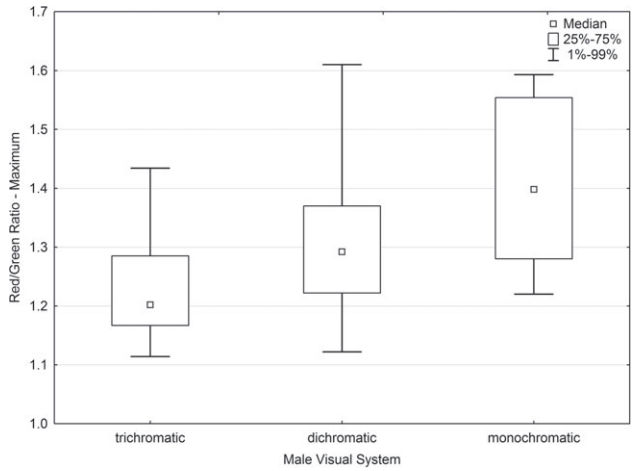

Fig. 4. Variation in the presence of red hair for primate species categorized by male visual systems. The redness of hair is quantified by the maximum Red/Green ratio sampled at any location on the pelage.

significantly redder than trichromatic primates in all three models (monochromatic species—model 2: PGLS, estimate = 0.153, $P < 0.01$, $n = 92$; model 3: PGLS, estimate = 0.162, $P < 0.01$, $n = 92$; model 4: PGLS, estimate = 0.143, $P < 0.01$, $n = 92$ and dichromatic species—model 2: PGLS, estimate = 0.099, $P = 0.001$, $n = 92$; model 3: PGLS, estimate = 0.098, $P < 0.001$, $n = 92$; model 4: PGLS, estimate = 0.091, $P < 0.001$, $n = 92$). Pagel's lambda was zero in all models.

When we used the mean Red/Green ratio data set, we found two equally good models according to AICc scores (Table III). Monochromatic species were significantly redder than trichromatic species in two models. Dichromatic species tended to be redder than trichromatic species in these same models (Table III). Pagel's lambda varied in the mean Red/Green ratio models from 0.448 to 0.487.

The variables "time since collection" and "body mass dimorphism" were not significantly related to either the mean or maximum Red/Green ratio values in any of the VS models. For time since collection, P values ranged from 0.05 (with a slope in the opposite direction expected) to 0.73 in female models and 0.07 (with a slope in the opposite direction expected) to 0.76 in male models. For body mass dimorphism, P values ranged from 0.64 to 0.95 in female models and 0.62 to 0.98 in male models. Similarly, the variable "activity pattern" was not significant in any of the visual models, indicating that the increased reddishness of di- and monochromatic species is not related to a nocturnal environment. For this

variable, *P* values ranged from 0.16 to 0.59 in female models and 0.34 to 0.57 in male models.

DISCUSSION

The goal of this study was to test whether trichromatic color vision either coevolved with or served as an exaptation for the evolution of red colored pelages in various primate higher taxonomic groups. In contradiction to the predictions of either of these hypotheses, our results demonstrate that the hair color of trichromatic primates is not more likely to exhibit a red hue compared to other primates. Not one of our models, all of which utilized phylogenetically controlled comparisons, demonstrated statistical support for routine trichromatic species possessing redder pelage than mono- or dichromatic taxa. In many cases, species with monochromatic or dichromatic VSs were found to have redder pelages than trichromats. Moreover, polymorphic species were found to possess redder pelages than routine trichromats in several models based upon either mean or maximum red/green ratio. It is important to note that this latter result is based upon female VS analyses; males of taxa with polymorphic trichromacy are unable to distinguish the red color signal.

Our results contradict the hypothesis advanced by Fernandez and Morris [2007] that linked the timing and phylogenetic distribution of red hair across primates with the emergence of trichromatic color vision. Instead, the evolution of the red color channel may have led to a reduction or loss of redder pelages among primates with routine trichromacy. We suggest that our results differ from this earlier study because we employ a more representative and up-to-date hypothesis of primate phylogenetic relationships, quantitative data on pelage coloration that sampled multiple relevant sites across the research skin, and a corrected scoring of strepsirrhine color vision phenotypes [see Bradley & Mundy, 2008].

Although our results do not support a relationship between red pelage and trichromacy, our data certainly highlight the frequent convergent evolution of pelage coloration in primates (see Fig. S2). That red pelage coloration is an evolutionary labile and reoccurring trait is not surprising. Convergent patterns of pelage coloration often [Hubbard et al., 2010], but not always [Bradley et al., 2012; Mundy & Kelly, 2003] come about via convergent genetic mechanisms. For example, light-colored hair in the woolly mammoth and in the Florida beach mouse is a product of the same convergent single-nucleotide mutation (arginine-to-cysteine substitution) effecting the same amino acid position in the pigmentation gene *MC1R* [Hoekstra et al., 2006; Rompler et al., 2006].

One possible explanation for our unexpected results (i.e., lack of association between red hair pigmentation and trichromacy) is that primate pelage coloration is strongly driven by selection pressures other than conspecific signaling. For example, we have previously shown [Kamilar & Bradley, 2011b] that variation in pelage darkness is correlated with aspects of habitat and climate, such as relative humidity [Gloger, 1833]. The underlying causes of this relationship are unknown, but camouflage in relatively dark forest environments likely plays a role.

Indeed, camouflage seems to be a major contributing component to primate coloration. A possible form of camouflage employed by primates is "background matching"—the matching of chromatic cues as well as achromatic features (such as light intensity) between the animal and the background [Endler, 1978; Merilaita & Stevens, 2011; Ruxton et al., 2004]. Existing research on primate coloration suggests that at least some aspects of primate hair color diversity are related to increasing crypsis. Kamilar [2009] and Kamilar and Bradley [2011a] showed that small primates exhibit stronger countershading (i.e., a light ventral surface and dark dorsal surface) compared to large species. One mechanism of countershading that may increase crypsis is background matching. A strongly countershaded arboreal primate with a light-colored ventral surface may appear to blend into a bright sky from the perspective of a ground-dwelling predator from below. Alternatively, the dark dorsal surface of this primate would appear to match the dark understory from the perspective of an avian predator from above.

Whether background matching is effective is entirely dependent upon the features of the VS of the viewer. Most carnivorans (e.g., felids) are probably dichromatic based upon the known distribution of opsins in the few taxa that have been studied [Jacobs, 1993, 2009]. For example, if that dichromatic carnivoran were looking at an arboreal primate with red dominant coloration, what looks like red to a trichromat would likely appear just dark to that carnivoran. The dark pelage would blend effectively with the green background foliage, also seen as dark, and therefore red would provide that primate with effective camouflage. If snakes also possess dichromatic vision [e.g., Davies et al., 2009], then these taxa would also have difficulty discriminating reds from dark green backgrounds. Though, snakes may also employ nonvisual senses to frequently detect potential prey animals [Isbell, 2009; but see Wheeler et al., 2011]. In contrast to carnivorans and snakes, diurnal avian predators, which are tetrachromatic like many nonmammalian vertebrates [e.g., Hart, 2001; Jacobs, 2009], likely discriminate along the red-green spectrum and break the color match to the background of a red pelage. Although the relationship between spectral sensitivities and ability to detect camouflage are complex [Morgan et al., 1992], it is reasonable to hypothesize that in some primate taxa reddish pelage coloration evolved as a part of a cryptic strategy for predator

avoidance. In order to evaluate the background matching of primate coloration, data are required on wavelengths reflected by both the species and the predominant background that they inhabit. Most importantly, receptor modeling is required of the various predators that prey upon primates specific to that environment relative to primate coloration and their actual natural environment/background [e.g., Osorio & Vorobyev, 2008].

Future work on this topic could expand this analysis in several directions. Although we feel confident that our data set captures a significant amount of interspecific variation in primate hair color, it is not exhaustive. For example, forest guenons (*Cercopithecus* spp.) and tamarins (*Saguinus* spp.) exhibit a diverse array of hair color patterns [Groves, 2001; Hershkovitz, 1977; Kingdon, 1988]. Our current data set includes several species within each group, but broader sampling within these genera would be worthwhile.

In addition, our study focuses on broad interspecific patterns, yet intraspecific variation is well known for several primate species, both in terms of sexual dichromatism and across-population variation. Sexually dichromatic primates vary in the type of color variation between the sexes. In contrast to the common pattern in birds [Andersson, 1994; Hill, 2006], males of sexually dichromatic primate species are not necessarily brighter than females [Bradley & Mundy, 2008]. For instance, *Eulemur rubriventer* males exhibit a redder belly than females, though *E. macacao* males are nearly uniformly black, while females are combination of white, gray, and brownish red. Also, geographic variation in hair color is well known for several primates. For instance, although black and white ruffed lemurs (*Varecia variegata*) exhibit predominantly black and white hair patches, many individuals also display noticeable brownish-red patches. Interestingly, these patches vary substantially in size and frequency across populations [Mittermeier et al., 2010].

We employed two methods for quantifying the amount of red hair exhibited by species. We found that there were greater differences among species with different VSs when we used the maximum Red/Green values compared to the mean value across specimen sampling locations. This may be due to correlated color patterns across sampling locations that would influence the mean Red/Green values. For instance, we quantified color at four locations on the dorsal side of the fore- and hindlimbs. For many primates, these sampling locations exhibit similar color patterns. If these locations display nonred hair, then this may swamp out red patches found at other parts of the body.

It is especially notable that we did not find a statistically significant effect for time since collection on the redness of primate hair. One potential concern for studies of museum research skins is the possibility of ultraviolet damage to the hair leading to degradation of hair color. We controlled for this factor, in part, by restricting our data collection to those research skins that had been properly stored, and by avoiding specimens that had been exposed to ambient light as part of a public display. Our findings support our previous results [Kamilar & Bradley, 2011b] that time since collection is not a factor that should preclude color-based data collection on research skins that have been properly stored. This is reassuring considering the traditional and extensive use of museum research skins in primate taxonomy [e.g., Groves, 2001; Hershkovitz, 1977].

Lastly, we would like to emphasize that, although red pelage coloration does not appear to have evolved for sociosexual signaling across primates, alternative red signals may have. We cannot eliminate the possibility that red skin color may be more important than hair color for interindividual relationships, particularly in catarrhines where red-skin sexual traits are extremely salient physical features with a clear role in sociosexual signaling. The notable example of red sexual swellings, which are only found in catarrhines (all of whom are routine trichromats), argues for some exploitation of red as a primate visual signal.

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