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Sexual Selection and Trichromatic Color Vision in Primates: Statistical Support for the Preexisting-Bias Hypothesis

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ABSTRACT: The evolution of trichromatic color vision in primates may improve foraging performance as well as intraspecific communication; however, the context in which color vision initially evolved is unknown. We statistically examined the hypothesis that trichromatic color vision in primates represents a preexisting bias for the evolution of red coloration (pelage and/or skin) through sexual selection. Our analyses show that trichromatic color vision evolved before red pelage and red skin, as well as before gregarious mating systems that would promote sexual selection for visual traits and other forms of intraspecific communication via red traits. We also determined that both red pelage and red skin were more likely to evolve in the presence of color vision and mating systems that promote sexual selection. These results provide statistical support for the hypothesis that trichromatic color vision in primates evolved in a context other than intraspecific communication with red traits, most likely foraging performance, but, once evolved, represented a preexisting bias that promoted the evolution of red traits through sexual selection.

Keywords: sexual selection, preexisting bias, trichromatic color vision, foraging.

Many primates possess trichromatic color vision, which allows them to fully discriminate the visible light spectrum. Because trichromatic color vision is absent in other eutherian mammals, there has been considerable interest in the evolutionary origin of this trait. The foraging hypothesis suggests that primates with enhanced (i.e., trichromatic) color vision are more efficient at detecting certain

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red/orange food items against a background of leaves than dichromatic individuals, who possess "red-green" color-blindness (reviewed by Surridge et al. [2003]). Theoretical studies have shown that trichromatic phenotypes are better suited than dichromats for distinguishing ripe-fruit hues (red, orange, and yellow; Osorio and Vorobyev 1996; Regan et al. 2001; but see Riba-Hernández et al. 2004) and young red leaves (Lucas et al. 1998, 2003) from nonripe fruits and leaf background. However, some field studies have failed to find that trichromatic individuals are more efficient foragers (Dominy et al. 2003a) or that they prefer red fruits over green cryptic fruits (Dominy 2004).

Recently, several studies have noted that primates use colors of high chroma and saturation (e.g., red) for intraspecific signaling in a sociosexual context (Setchell and Dixson 2001; Waitt et al. 2003; Setchell and Wickings 2005; Changizi et al. 2006; Setchell et al. 2006). Changizi et al. (2006) suggested that because enhanced color vision in some primates is nearly optimal for discriminating skin color modulations and variations in blood oxygen saturation, this supports the hypothesis that trichromacy was originally selected for the perception of skin color signaling. However, current function does not necessarily confer historical genesis (Gould and Vrba 1982; Greene 1986; Baum and Larson 1991). Determining the performance advantage that initially selected for trichromatic color vision in primates requires evidence of phylogenetic congruence between the origin of trichromatic color vision and the measured performance advantage (Greene 1986).

More than a century ago, it was suggested that trichromatic color vision in primates, once evolved, could be "recruited" for other purposes (e.g., sexual signaling; Allen 1879). The preexisting-bias hypothesis suggests that mating preferences for particular traits evolve before the traits, with traits evolving later to take advantage of the bias (Basolo 1990; Endler and Basolo 1998). This general hypothesis, which includes the idea of sensory traps (e.g., Christy 1995), explains the initial evolution of mating preferences as sensory functions that switch from a context other than sexual selection to the context of mating preferences (Endler and Basolo 1998). Receiver-bias models

differ from the classical sexual-selection models (i.e., Fisher's runaway and "good genes"; see Kirkpatrick and Ryan 1991) in that they focus on the origin of a preference, not its subsequent evolution. Therefore, establishing the sequential evolution of the trait and the preference using a robust phylogenetic comparative method is crucial for evaluating the preexisting-bias hypothesis. Phylogenetic support for the preexisting-bias hypothesis has been limited (e.g., swordtails: Basolo 1990, 1995, 1996; tungara frogs: Ryan and Rand 1990, 1993; damselflies: Córdoba-Aguilar 2002). In addition, the only statistical test of this hypothesis was presented as an example of reconstructing ancestral states with maximum likelihood (Schluter et al. 1997), and the support was not statistically significant.

Here, we examine the hypothesis that the presence of trichromatic vision in certain lineages of primates represents a preexisting bias for colors of high chroma and saturation that, once present, would facilitate the evolution of red-orange traits in these species through sexual selection. For the data to support the preexisting-bias hypothesis, our analyses should show that trichromacy evolved before red pelage and red skin and that red pelage and red skin were more likely to evolve on those branches that have this bias (trichromacy). In addition, assessment of visual traits would be facilitated in more gregarious social systems, in which sexual selection is thought to be stronger (Andersson 1994). Therefore, further support of the importance of sexual selection in the evolution of red traits in primates would include evidence that red pelage and red skin were more likely to evolve on branches of the phylogeny that have both trichromatic color vision and gregarious mating systems.

Material and Methods

We collected data on four characters—color vision, pelage color, the presence or absence of red skin, and mating systems—from a large variety of literature sources (see app. B in the online edition of the *American Naturalist* for sources) for the 203 taxa included in the Purvis "supertree" phylogeny of primates (Purvis 1995). The Purvis phylogeny is a composite of more than 100 previous estimates (i.e., source trees) and was derived through matrix representation using parsimony (Baum 1992; Ragan 1992). The tree is relatively well resolved, with 160 nodes that have, on average, high bootstrap values (range = 11–100; mean = 68.2) and therefore has been frequently used in phylogenetic comparative analysis (Nunn and Barton 2001; Anderson et al. 2004). To statistically test the preexisting-bias hypothesis and its applicability to the primate order, as well as the potential role of intraspecific communication in the initial evolution of trichromatic color vision in primates, we first determined the sequential evolution of four traits (color vision, skin color, pelage color, and social systems) by employing two ancestral-state reconstruction methods, one that uses maximum parsimony and one that uses maximum likelihood. Subsequently, we used two phylogenetically based methods, one based on maximum parsimony (concentrated-changes tests [CCTs]) and the other on maximum likelihood (contingent-change tests), to examine the coevolution of trichromatic color vision in relation to the other three traits. These correlated evolution analyses allowed us to determine whether red traits and gregarious mating systems that promote sexual selection on visual traits were more likely to have evolved in the presence of trichromatic color vision, consistent with the preexisting-bias hypothesis.

Character Scoring

The scoring of the all characters was cross-referenced with at least two sources before the assignment of a binary character state for that taxon (see app. B for sources).

Color vision. The categorization of visual systems for all taxa in the Purvis phylogeny was obtained from several sources (Jacobs 1998, 2002; Jacobs and Deegan 1999, 2001, 2003; Surridge et al. 2003). The degree of visual capacity for each species was transformed into a binary character. Taxa with monochromatic or dichromatic vision were scored as 0, whereas taxa with allelic and routine trichromatic vision were scored as 1.

Within the strepsirrhine clade (lemurs and lorises), a few species have been discovered with separate M and L cones (Tan and Li 1999); therefore, it is believed they possess red-green color discrimination. These taxa were not represented among the 203 species in the phylogeny by Purvis (1995) and thus were not incorporated in our analysis. In addition, note that we incorporate recent evidence suggesting that Tarsiidae have some form of red-green color discrimination (Tan and Li 1999; Hendrickson et al. 2000; Collins et al. 2005). In light of these findings, we scored all four species of tarsiers in the Purvis phylogeny as having trichromatic vision (i.e., as 1). For completeness, however, we also performed the ancestral-state reconstruction of color vision and all correlated evolution analyses with the alternative scoring of Tarsiidae (i.e., lacking trichromatic color vision, or 0).

Mating systems. The classification of mating systems followed Dixson (1998), where the primary mating system was reported, excluding the secondary mating systems and mating tactics. Given the complexity of primate mating systems, we considered gregarious or social systems to be more likely conduits for sexual selection of visual signals than nonsocial systems and scored this as a binary character by grouping multimale-multifemale and polygynous systems (scored as 1), whereas monogamous and solitary

systems were scored as 0. Although research has shown that "solitary" taxa often communicate in social networks via olfactory and vocal displays (Charles-Dominique 1977; Bearder 1987), our classification of "gregarious" is focused on situations in which sexual selection would promote the evolution of visual signals in communication. With the exception of one great ape species (orangutan *Pongo pygmaeus*), all primates with solitary mating systems are nocturnal prosimians in which visual communication is not the primary means of communication (Dixson 1998).

In numerous taxa characterized as polygynous (e.g., proboscis monkey *Nasalis larvatus* and Gelada baboon *Theropithecus gelada*), multimale-multifemale systems are also common (Tattersall 1982; Dixson 1998). None of these polymorphic breeding systems affected the outcome of either of the correlated evolution tests because both mating systems were scored as the same character state, further justifying our choice of binary character classification for primate mating systems. In species for which mating system information was unavailable, we scored that taxon in accordance with the other members of the genus.

Pelage color. Classification of pelage color was based on the original qualitative description of a given taxon (see app. B for sources). If an author described a taxon with two colors, for example, red and brown, we classified the pelage color as the first hue recorded. If the description stated "reddish brown," we reported the pelage as "brown" and treated the suffix "-ish " as indicating only a "touch or trace of," as per Webster's Dictionary. This methodology is consistent with previously published research in which the authors attempted to standardize qualitative color descriptions from literature resources (Dominy et al. 2003*b*).

Numerous studies have shown that trichromatic color vision, as opposed to mono- or dichromatic, is superior, if not optimized, for distinguishing yellow, orange, and red targets against mature green foliage (Osorio and Vorobyev 1996; Sumner and Mollon 2000; Párraga et al. 2002). Thus, we scored taxonomic groups with these three hues (yellow, orange, and red) in their pelage as 1 and taxa with other hues as 0. In less than 4% of the taxa, pelage color was stated as being "highly variable" or no information was reported about coat color. In these cases, we scored the trait as ancestral (i.e., 0, or absent). With respect to the correlated evolution of this trait, this is a conservative approach, because every case in which information about pelage coloration was absent occurred in species that had trichromatic color vision.

Skin color. We chose to consider the presence of red naked skin as the trait of interest, regardless of location on the body (e.g., facial skin was categorized the same as genitalic skin), because our primary interest was to determine whether the discriminatory ability of trichromatic vision enhanced the evolution of red skin, regardless of

the potential information contained in the signal. If an author reported "light" or "pinkish" skin color (or a hue other than red), we scored that taxon as 0, and we scored the taxon as 1 only if red naked skin was reported.

Phylogenetic Analysis

Reconstruction of ancestral character states. We reconstructed the ancestral states for all four characters using maximum parsimony as implemented in MacClade 3.0 (Maddison and Maddison 1992) and maximum likelihood as implemented in Mesquite 1.06 (Maddison and Maddison 2005). Since the phylogenetic tree we used is a composite from studies using different kinds of data, no comparable branch lengths are available. Therefore, we used two sets of arbitrary branch lengths: all equal and Pagel branch lengths, which makes all terminal taxa contemporary (Pagel 1992), implemented in Mesquite within the PDTREE module (Garland et al. 1999). We used the Mk1 model of evolution in the maximum likelihood analysis, which treats changes between all character states as equally likely (Schluter et al. 1997). To determine whether there was statistical support for the ancestral state reconstructions, we used a likelihood decision threshold of $T = 2$, indicating support at least 7.4 times greater for that state than for the other state (Schluter et al. 1997).

Tests of correlated evolution. The question of whether red traits are more likely to evolve in the presence of color vision and gregarious mating systems was tested using methods based on maximum parsimony and maximum likelihood. The concentrated-changes test (CCT) is based on parsimony and determines whether origins (and/or losses) of one trait are significantly more likely to occur on branches in which the second trait is present (Maddison 1990). In order to execute a CCT, a fully bifurcating tree is necessary, yet the primate phylogeny we used had numerous multifurcations. These polytomies were resolved in two ways, once to produce the minimum number of gains in the dependent character state of interest and again to produce the minimum number of losses in the dependent character state of interest, so that our results would be robust to any biases due to the number of gains or losses of the dependent character being tested. Subsequently, any remaining polytomies in which the character of interest did not change were resolved randomly using MacClade. We mapped the independent trait onto each of the resultant bifurcating tree topologies (each dependent character had two tree reconstructions: minimum losses and minimum gains) and conducted a CCT for each. We ran 1,000 simulations for each analysis, using the "actual changes" option. Note that our approach of utilizing minimum number of gains and losses allows us to determine the robustness of our results to different phylogenetic res-

olutions of the polytomies in the Purvis (1995) phylogeny. Finally, for all statistical analyses, both gains and losses were considered.

We compared our results from CCTs to similar analyses using contingent-change tests based on comparing maximum likelihoods, implemented in Discrete 4.0 (Pagel 2000). We used the randomly resolved tree with all branch lengths equal as well as the randomly resolved tree with Pagel branch lengths, and we compared the likelihoods when q_{12} and q_{34} were equal (null hypothesis) to the likelihoods when they differed with a χ^2 goodness-of-fit test (Pagel 1994, 1999).

For both the maximum parsimony and maximum likelihood analyses, we conducted two different sets of comparisons. First, we selected color vision as the independent character and compared the correlated evolution of the three dependent variables (mating system, pelage color, and skin color). Second, we combined color vision and mating system as the independent character and compared the correlated evolution of this composite trait with red pelage and red skin. In these analyses, the presence of both gregarious mating system and trichromatic color vision (i.e., scores of 1 and 1) in a single species was considered to be the independent character state of interest and scored as 1. In other words, if a species was trichromatic but lacked a gregarious mating system or if a species was gregarious but lacked trichromatic vision, that species was scored as 0.

Results

Reconstruction of Ancestral Character States

Reconstructions of the ancestral states under maximum parsimony indicate that trichromatic color vision evolved at the ancestor to extant Tarsiidae-platyrrhine-catarrhine species (node 2, fig. 1) before the evolution of gregarious mating systems, red skin, and red pelage, all three of which evolved at the node giving rise to the Old World monkeys in all but one analysis (see figs. A1–A6 in the online edition of the *American Naturalist*). The analysis of red pelage using the minimum-gain tree topology suggests that red pelage evolved even later, at the node giving rise to the clade containing the *Cercopithecus* genus (see fig. A7 in the online edition of the *American Naturalist*). The maximum likelihood analyses using equal branch lengths also indicated that trichromatic color vision evolved before the other three characters (fig. 1). The most likely ancestral state at node 2 (the ancestor to extant Tarsiidae-platyrrhine-catarrhine species; see fig. 1) is trichromatic color vision present with the other three characters absent (table 1). The results using Pagel branch lengths supported the same order of character evolution; however, these results

were statistically significant for the presence of trichromatic color vision and absence of red skin color only at nodes 1, 2 and 3 and for the presence of gregarious mating system only at node 4 (table 1).

Reconstruction of the ancestral character state for the composite trait, color vision and mating system, under maximum parsimony suggested that species with both trichromatic color vision and gregarious mating systems evolved at node 4 (ancestor to the two extant subfamilies; see fig. A8 in the online edition of the *American Naturalist*). Maximum parsimony ancestral reconstruction for the trait red skin also indicated that red skin evolved at node 4, whereas red pelage evolved later, at the node giving rise to the clade containing the *Cercopithecus* genus (see figs. A9, A10, respectively, in the online edition of the *American Naturalist*). However, ancestral-state reconstruction using maximum likelihood supported the evolution of the composite trait preceding the evolution of red pelage and red skin, with the composite trait evolving at node 4 and the two red-coloration phenotypes evolving later than this. This sequence of ancestral-state reconstruction was the same regardless of scoring branch lengths as equal or using Pagel branch lengths.

Contingent Evolution

Results from the CCT analyses suggested that in those lineages with trichromatic color vision, both red pelage and gregarious mating systems evolved more frequently than expected by chance alone (table 2). The results for red skin were not statistically significant, but the trend was in the same direction (lack of significance possibly due to insufficient power; red skin had half as many steps as pelage). The contingent-change test, based on maximum likelihood, suggested that both red skin and red pelage were more likely to evolve in those lineages with trichromatic color vision, but only the result for evolution of red skin was statistically significant (table 3). These results suggest that the presence of color vision may have been necessary for the evolution of both red pelage and red skin in primates. In addition, these results suggest that in those lineages with trichromatic color vision, gregarious mating systems are more likely to evolve as well.

The CCTs for the second series of analyses, which considered the composite trait of color vision and gregarious mating systems as the independent character, suggested that in those lineages with trichromatic color vision and gregarious mating systems, both red pelage and red skin evolved more frequently than expected by chance alone (table 2). However, it should be noted that identifying the composite trait as the independent character (i.e., as having evolved before red skin) was not supported by the parsimony analysis. The contingent-change tests, based on
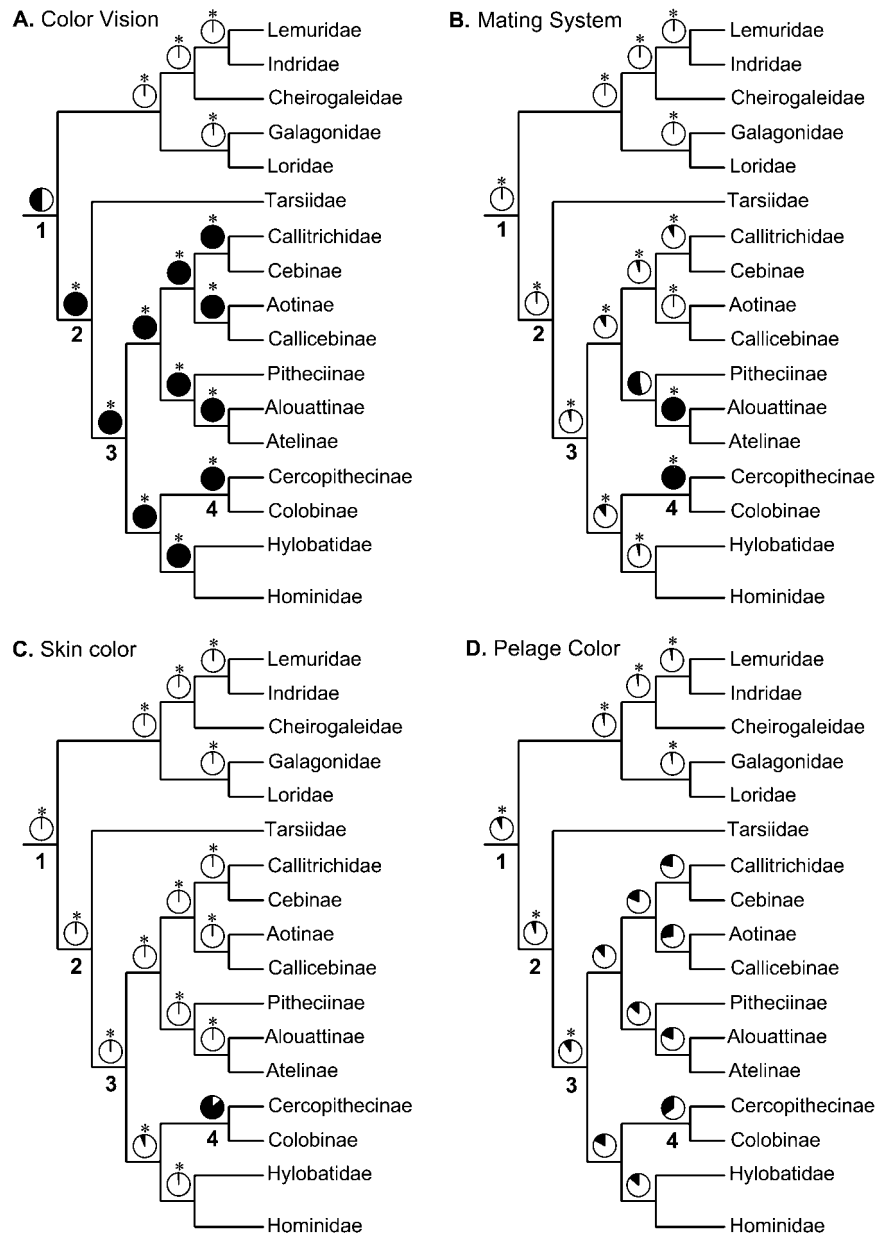
Figure 1: Ancestral-state reconstruction using maximum likelihood and the stored Mk1 model (i.e., equal likelihood) implemented in Mesquite (Maddison and Maddison 2005). Areas of pies indicate relative support for ancestral states. *A*, Color vision: presence of trichromatic color vision indicated in black; dichromatic/monochromatic indicated in white. *B*, Mating system: gregarious (multimale/multifemale, polygynous) indicated in black; nongregarious (solitary, monogamous) indicated in white. *C*, Skin color: presence of red skin indicated in black; absence of red skin indicated in white. *D*, Pelage color: presence of red pelage indicated in black; absence of red pelage indicated in white. Pie charts with asterisks indicate significant support for ancestral-state reconstruction at that node.

maximum likelihood comparisons, support these results as well (table 3). The likelihoods of red skin and red pelage evolving in those lineages with both color vision and gregarious mating systems were statistically significant. Therefore, these results support our hypothesis that social mat-

ing systems would exacerbate the evolution of red phenotypic traits that could be used as sexually selected signals in species with trichromatic color vision. Finally, regardless of how the visual capacity of Tarsiidae was scored (i.e., dichromatic or trichromatic), the results were

Table 1: Ancestral state reconstruction using maximum likelihood method for key nodes

Branch lengths, character	Node 1		Node 2		Node 3		Node 4	
	Absent	Present	Absent	Present	Absent	Present	Absent	Present
Equal:								
Color vision	.5	.5	.003	**.997**	.001	**.999**	.001	**.999**
Pelage color	**.928**	.072	**.95**	.05	**.904**	.096	.649	.351
Skin color	**.995**	.005	**.999**	.001	**.995**	.005	.14	.86
Mating system	**.997**	.003	**.996**	.004	**.948**	.052	.033	**.967**
Color vision–mating system	**.999**	.001	**.999**	.001	**.969**	.031	.02	**.98**
Pagel:								
Color vision	.095	**.905**	.005	**.995**	.001	**.999**	.001	**.999**
Pelage color	.529	.471	.53	.47	.532	.468	.538	.462
Skin color	**.899**	.101	**.904**	.096	**.897**	.103	.709	.291
Mating system	.78	.22	.762	.238	.698	.302	.066	**.934**
Color vision–mating system	**.911**	.089	**.904**	.096	.859	.141	.048	**.952**

Note: Node numbers are indicated in figure 1. Values represent relative likelihoods and are based on maximum likelihood estimates using the Mk1 model of evolution. Values in bold indicate significant support for the presence/absence of that character ($P < .05$), based on a likelihood threshold of $T = 2$ (support at least 7.4 times as great for that state as for the converse; Schluter et al. 1997).

the same; all of the correlation analyses were statistically significant (results not shown).

Discussion

The evolution of trichromatic color vision within primates has been attributed to both increased performance in foraging and interspecific communication. A phylogenetic analysis can distinguish between these two hypotheses (Greene 1986), and a maximum likelihood approach to ancestral reconstructions can estimate the uncertainty of the conclusions (e.g., Schluter et al. 1997). We present here the first statistical support of the preexisting-bias hypothesis. If trichromatic color vision in primates were a preexisting bias for the evolution of red traits, we would expect trichromacy to have evolved before red traits. Ancestral reconstructions based on both maximum parsimony and maximum likelihood suggest that trichromatic color vision evolved before red pelage and red skin. In addition, analyses that examined contingent evolution provided further statistical support that red traits in primates were more likely to evolve in lineages with color vision. Finally, demonstrating that both pelage and skin color were significantly more likely to evolve in lineages with both a gregarious mating system and color vision provides even stronger support for our hypothesis that sexual selection enabled by advanced visual capacity has promoted the evolution of phenotypic traits with high chroma and saturation. While sexual selection is likely to have been acting in primates before the evolution of social mating systems, the close proximity of individuals in social mating systems would facilitate comparison of mates and/ or competitors through visual signaling.

The significant correlation we detected between gregar-

iousness and trichromatic vision suggests that enhanced color vision may have played a role in the evolution of gregariousness. The relationship between trichromatic color vision and gregariousness may also provide insight into recent studies on the degeneration of the vomeronasal organ (VNO) in some species of primates (Liman and Innan 2003; Gilad et al. 2004). Interestingly, research has shown that the evolution of routine trichromacy (both males and females have trichromacy) in Old World monkeys and apes coincided with the loss of a functioning VNO (Liman and Innan 2003). Liman and Innan (2003) suggest that Old World monkeys and apes, the majority of which are gregarious, became less reliant on chemosensory communication with the development of visual signals for intraspecific communication. Our phylogenetic analyses lend further support to their assertion and suggest that red pelage and red skin are likely to serve as visual signals in those species that no longer use scent as their primary form of sociosexual communication. The propagation of olfactory signals differs in several ways from the propagation of visual signals (Bradbury and Vehrencamp 1998), and therefore this shift from chemical to visual communication is likely to be an important component of the evolution of gregariousness in primates. It is noteworthy that prosimians, the majority of which lack trichromacy, have retained VNO function and utilize olfactory communication extensively (Evans and Schilling 1995; Aujard 1997; Gilad et al. 2004), even those species that are gregarious (e.g., male "stink fights" in dichromatic ring-tailed lemur *Lemur catta*; Jolly 1966).

The number of studies providing direct evidence for sexual selection on red traits in primates continues to grow. Recent behavioral studies examining female mate choice in primates have found that red facial skin is preferred

Table 2: Summary of concentrated-changes tests (CCTs) based on maximum parsimony

Independent character, dependent character	Criteria for topological construction[a]	Range of probabilities[b]
Color vision:		
Pelage color	Min. gains*	.012–.033
	Min. losses**	.006–.013
Skin color	Min. gains	.076–.081
	Min. losses	.073–.119
Mating system	Min. gains*	.001–.044
	Min. losses*	.001–.050
Color vision–mating system:		
Pelage color	Min. gains**	.009–.012
	Min. losses**	.001–.007
Skin color	Min. gains**	.006–.012
	Min. losses**	.006–.017

[a] To obtain a fully bifurcating tree, polytomies were resolved to produce either the minimum number of gains in the dependent character state of interest or the minimum number of losses in the dependent character state of interest. Polytomies in which no character state change occurred were randomly resolved in MacClade 3.0 (Maddison and Maddison 1992).

[b] Based on resolving equivocal states both possible ways (i.e., a separate CCT was conducted for each state of the dependent character at that node).

  * $P < .05$.

  ** $P < .01$.

over paler ones, possibly providing information about mate quality (Waitt et al. 2003; Setchell 2005). Red sexual skin is most common in Old World monkeys, the majority of which have gregarious mating systems (Dixson 1998). Although the role of sexual skin in sociosexual communication is not a new concept (Dixson 1983; Bielert and Anderson 1985), the inclusion of red pelage as a possible sexually selected signal is relatively new (for a review, see Sumner and Mollon 2003). The potential role of red pelage as a sexually selected signal is most evident in a species of langur from southeast Asia, *Presbytis geei* (golden leaf monkey), which experiences seasonal variability in pelage color. Adult males and females are creamy white in color during the nonbreeding season but become bright red during the winter breeding season (Khajuria 1977).

The lack of sexual dimorphism in pelage color within many trichromatic primate species does not necessarily suggest that this trait is not under sexual selection (Andersson 1994). Within primates, there is growing evidence and interest in male mate choice in primates because males of many species experience costs associated with mate choice (e.g., in Old World monkeys, male aggression and competition: Domb and Pagel 2001; Setchell and Wickings 2006; in marmosets and tamarins, male parental care: Sanchez et al. 1999; Achenbach and Snowdon 2002). Recently,

it has been shown in mandrills (*Mandrillus sphinx*), a species with intense male-male competition, that the intensity of red facial skin serves not only as a visual signal of male competitive ability (Setchell and Dixson 2001; Setchell and Wickings 2005) but also as a potential signal of female reproductive quality (Setchell et al. 2006). However, in addition to sexual selection, red pelage could have other roles in gregarious mating systems that would be consistent with our results. One possibility is that red pelage plays a role in the maintenance of group cohesion while moving and/or feeding through the forest canopy (Sumner and Mollon 2003). In addition to the benefits of adults with red pelage, numerous studies have suggested social benefits to the orange pelage in the young of some catarrhine species (encouraging allocare: Hrdy 1976; Ross and Regan 2000; guarding against infanticide: Treves 1997). In summary, our results strongly suggest that trichromatic color vision did not evolve in the context of intraspecific communication via red traits (be it group cohesion or sexual selection). While evidence for sexual selection on red traits continues to grow, further studies are needed to determine the specific sociosexual selection driving the evolution of specific red traits in primates.

A preexisting bias for the sexually selected caudal extension in swordtail fishes can be found in both sexes, and

Table 3: Summary of contingent-change tests based on maximum likelihood

Branch length, character 1, character 2	Maximum likelihood ratio[a]	df	P
Equal:			
Color vision:			
Pelage color	2.73	1	.098
Skin color	5.95*	1	.015
Mating system	8.00**	1	.005
Color vision–mating system:			
Pelage color	7.22**	1	.007
Skin color	10.71**	1	.001
Pagel:			
Color vision:			
Pelage color	1.54	1	.213
Skin color	4.33*	1	.037
Mating system	13.16**	1	<.001
Color vision–mating system:			
Pelage color	9.87**	1	.002
Skin color	16.02**	1	.001

[a] Based on comparison of the likelihoods when q_{12} and q_{34} were equal (null hypothesis) and the likelihoods when they differed with a χ^2 goodness-of-fit test (Pagel 1994).

  * $P < .05$.

  ** $P < .01$.

it has been suggested that this indicates a shared ancestral bias in males and females (Basolo 2002). If the evolution of red pelage was the result of a preexisting bias for red food items, then one might expect both males and females to have evolved the bias. However, the classification of some primates in the most ancestral clade (i.e., strepsirrhine) as having allelic trichromatic color vision (heterozygous females trichromatic, homozygous females and all males dichromatic; Tan and Li 1999; Jacobs et al. 2002) suggests that color vision may have initially been sexually dimorphic. A recent study found that dichromatic non-human primates have a visual advantage over trichromatic individuals in discriminating color-camouflaged stimuli, which suggests a possible adaptive explanation for the visual dimorphism found in many extant primates (Saito et al. 2005). However, it will be interesting to examine those primates in which males and females differ in their degree of color vision in relation to sexual selection of red phenotypic traits.

A key component of the preexisting-bias hypothesis is that once a trait evolves to take advantage of the bias, the original preference can be maintained or modified from its original form (Endler and Basolo 1998). Therefore, if enhanced color vision, once evolved, was recruited for other purposes (e.g., mate choice and/or male-male competition), selection on this new function could alter aspects of color vision within the new context. This scenario for the evolution of trichromacy in primates would explain some of the equivocal support for the foraging-performance hypothesis (Dominy et al. 2003*a*; Smith et al. 2003). One might not expect all trichromatic primates to forage more efficiently on red food items if trichromacy initially evolved to increase foraging efficiency and is now maintained through sexual selection in those lineages in which the bias for red no longer functions to improve foraging efficiency.

Proponents of the foraging-efficiency hypothesis for the evolution of trichromacy have debated which type of food source was involved in the initial evolution of trichromatic color vision (red fruits: Polyak 1957; Mollon 1989; young red leaves: Lucas et al. 1998, 2003; Dominy and Lucas 2001). Variation in the foraging habits within the family Cercopithecidae (Old World monkeys) could potentially provide insight into this debate. The Cercopithecidae family is divided into two subfamilies: the predominately frugivorous Cercopithecinae (Fleagle 1998) and the Colobinae, which are well known as folivores (Davies and Oates 1995). However, vision research has shown that these two subfamilies with distinctly different foraging habits show no appreciable differences in their spectral sensitivities at the M and L cones and thus have uniformity of color vision (Jacobs and Deegan 1999). Interestingly, our optimization of red skin onto the Purvis phylogeny reveals that this trait evolved at the internal node before the divergence of the two subfamilies, providing a possible explanation for the conserved spectral sensitivities of the M and L cones within the Cercopithecidae despite their divergence in foraging niches. This explanation is consistent with recent work by Changizi et al. (2006) that showed that the maximum M- and L-cone sensitivities of trichromats are optimized for discriminating variations in blood oxygen saturation, a component of skin reflectance. In addition, our maximum parsimony and maximum likelihood ancestral reconstructions indicate that gregarious mating systems also evolved at the same internal node as red skin, suggesting that sociality and mate comparison might play a role in the maintenance of trichromatic vision in this group.

Finally, it might be asked why not all trichromatic primate species possess red pelage and skin. Red traits have not evolved in all lineages with trichromatic color vision, and in some groups with enhanced color vision, these traits appear to have been lost. There are several possible explanations for the lack of red phenotypic traits in extant primates. First, there may be a lack of the genetic variation necessary for the phenotype. Second, there may be a lack of the dietary supplements needed to produce these traits. Third, there may be intense predation pressure. The role of predation in the loss of sexually selected traits has been examined in the guppy (*Poecilia reticulata*). Predation pressure in some populations can lead to a loss of nuptial coloration (orange spots on males; Endler 1980), and variation in female preference is correlated with the presence or absence of this nuptial coloration (Endler and Houde 1995).

To our knowledge, this is the first application of the preexisting-bias hypothesis to primates and the first statistical support of this hypothesis. The relationship we detected between the evolution of gregarious mating systems that promote sexual selection for visual traits and that of red pelage and red skin support the growing lines of evidence that these traits play a role in sexual selection. However, our phylogenetic reconstruction revealed that red skin and red pelage, as well as gregariousness, evolved after trichromatic color vision. This sequential trait evolution was detected regardless of the phylogenetic ancestral-state reconstruction method used (i.e., maximum parsimony or maximum likelihood). Therefore, it is unlikely that trichromatic color vision evolved in the context of intraspecific communication; instead, it likely represents a preexisting bias that promoted the evolution of these red traits. Future studies are needed to further examine mate preferences for red pelage and red skin and advance our understanding of the role of red coloration as a component of intraspecific communication among trichromatic primate species.

Acknowledgments

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