Human Preferences for Colorful Birds: Vivid Colors or Pattern?

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Abstract: In a previous study, we found that the shape of a bird, rather than its color, plays a major role in the determination of human preferences. Thus, in the present study, we asked whether the preferences of human respondents towards uniformly shaped, colorful birds are determined by pattern rather than color. The experimental stimuli were pictures of small passerine birds of the family Pittidae possessing uniform shape but vivid coloration. We asked 200 participants to rank 43 colored and 43 identical, but grayscaled, pictures of birds. To find the traits determining human preferences, we performed GLM analysis in which we tried to explain the mean preference ranks and PC axes by the following explanatory variables: the overall lightness and saturation, edges (pattern), and the portion of each of the basic color hues. The results showed that the mean preference ranks of the grayscale set is explained mostly by the birds’ pattern, whereas the colored set ranking is mostly determined by the overall lightness. The effect of colors was weaker, but still significant, and revealed that people liked blue and green birds. We found no significant role of the color red, the perception of which was acquired relatively recently in evolution.

Keywords: coloration, human vision, perception, avian taxa, evolutionary psychology

Introduction

A large number of birds possess various conspicuous ornaments, e.g., contrasting or colorful spots and/or feathers such as the long tail feathers of some pheasants, quasals, or whydahs, the crests of cacatuias and turacos, or the colorful patterns of many parrots, toucans, and pittas (del Hoyo, Elliott, and Christie, 2003). These traits have evolved as a means of visual communication with their conspecifics, predators, and competitors, making their bearers the winners of the sexual and/or natural selection process (Andersson, 1994;
Bennett and Owens, 2002). Irrespective of the primary function of these traits in the microevolutionary ways to help the individuals survive and reproduce, a secondary function rises with the modern age strongly affected by pressure from mankind. Humans perceive certain traits as “beautiful” or “ugly” and treat their bearers accordingly. The “beautiful” animals are selectively kept by zoological gardens worldwide (Frynta et al., 2009; Frynta, Šimková, Lišková, and Landová, 2013), and these also receive more conservation-oriented attention by both public and federal funding (Metrick and Weitzman, 1996). It is thus important to ask which appearance traits are perceived and judged by humans as “beautiful.”

Colors have long been known to connect with human emotions and feelings, such as sadness or happiness (Gao et al., 2007), and this may in turn affect human preferences for certain colored animal traits. Saturated basic color hues of blue, green, and yellow are usually associated with positive feelings. The blue color is reported to evoke the feeling of calmness, restfulness, peace, security, and comfort; green is linked with peace, comfort, hope, and happiness; and yellow is perceived as joyful, lively, energetic, and cheerful (Ball, 1965; Crozier, 1997; Kaya and Epps, 2004). The color red, being more ambiguous, is sometimes perceived positively with emotions like love, happiness, and energy (Crozier, 1997; Kaya and Epps, 2004), but simultaneously evokes anger and hatred (Kaya and Epps, 2004; Mahnke, 1996). Red is also often reported to cause excitement and arousal (Elliot and Maier, 2007; Wilson, 1966; Wolfson and Case, 2000), enhance human performance in contests (Hill and Barton, 2005), and function as a distracter (Ioan et al., 2007), lessening a person’s concentration and performance (Elliot, Maier, Moller, Friedman, and Meinhart, 2007). From achromatic colors, only white is perceived positively, and this is true for people of both Western and Eastern traditions, despite the known fact that white is associated with death in China (Kaya and Epps, 2004; Saito, 1996). Black and grey colors are perceived negatively as depressive hues (Kaya and Epps, 2004), associated with sadness, hatred, mourning, and sorrow (Ball, 1965; Mahnke, 1996). These attributes of black (low lightness) and gray (low contrast) also cause a notable shift from positive to negative perception when mixed with otherwise positive hues, lowering peoples’ preferences for dark and dull colors, such as brown being less attractive compared to orange (Manav, 2007). Low lightness is also reported to cause people to feel less relaxed, and hues with low contrast elicit lower excitement (Gorn, Chattopadhyay, Yi, and Dahl, 1997).

According to the principle of linguistic relativity (linguistic determinism; Whorf and Carroll, 1956), human cognitive perception and categorization of colors is linked with the color terms existing in the languages of various cultures. This stimulated cross-cultural comparisons of color naming and perception (Berlin and Kay, 1969). Recently, Kay, Berlin, Maffi, Merrifield, and Cook (2010) performed a detailed study of 110 genetically diverse languages, which led them to recognize a certain universal pattern in the emergence of color terms in human languages. The first colors that are usually named, and thus distinguished, are black and white. This partition means that people recognize “light” and “dark” colors of any hue. The importance of black and white colors’ recognition in this partition may be influenced by the fact that objects are recognizable, even during a night (dark) environment, with illumination too low to stimulate hue sensation. The next rule for color terms partition as described by Kay et al. (2010) is the distinction of a warm and cool hue spectrum, with red, yellow, and its intermediates coming under the “warm” category
Human preferences for colorful birds

and with green, blue, and its intermediates coming under the “cold” category. This distinction is long-recognized by color specialists in the fields of both art and science, and it is also very interesting to note that the intermediate hue of yellow-green, which links together these dual spectra, affects human emotions negatively, evoking associations with sickness and disgust (Kaya and Epps, 2004). The third rule of forming color terms highlights the importance of the color red. As noted above, the emotional meaning of red hues is controversial, causing arousal and quickening heartbeat, which may point to a special importance of this color for human recognition. Altogether, the terms for the colors black, white, yellow, green, blue, and red, which are considered the basic hues, appear primarily, being followed by the terms for grey, brown, orange, pink, purple, and other possible intermediate and mixed colors (Kay et al., 2010).

The vivid colors of birds are meant to be seen by their conspecifics, which possess tetrachromatic vision, an ancestral evolutionary trait in terrestrial vertebrates (Bowmaker, 2008; Hart, Bailes, Vorobyev, Marshall, and Collin, 2008). But are humans, as members of the mammalian clade, able to see and appreciate the avian colors in full? During the mammalian ancestry of small and nocturnal animals, their color vision was reduced to a dichromatic state (Heesy and Hall, 2010; Zhao et al., 2009). Dichromatic vision is consistent with the warm-cool spectra discrimination, recognizing the short-wave spectrum on one side and long-wave spectrum on the other side (Jacobs, 2009). Humans and some other monkeys and apes (independently in Old World primates and New World howler monkeys) regained true trichromatic vision, but the third gene for opsin with sensitivity in long wavelengths (red) has evolved only recently when compared to the evolutionary history of mammals (see Martin and Ross, 2005, and references therein). In this light, we may ask about the importance of achromatic colors for human preferences as compared to blue, green, and yellow hues on one side (evolutionarily ancestral) and red on the other side (evolutionarily recent). If the origin of human emotions and preferences reaches far into the long ancestry of small nocturnal mammals, achromatic colors (consisting of variance in lightness and contrast and forming the base of patterns and shapes) should play a major role in assessing human aesthetic preferences. These would be followed by the ancestrally seen hues of blue, green, and yellow. On the other side, red is known as an exciting color causing arousal, important in primate communication (Setchell, Jean Wickings, and Knapp, 2006) and food gathering (Surridge, Osorio, and Mundy, 2003). Thus, the position of this color in human aesthetics forms a very interesting question.

In our previous studies, we showed that morphology and selected colors affected human preferences towards birds. In parrots, humans preferred long tails along with blue and yellow colors, while green color (present on most of the parrots in majority) affected preferences negatively (Frynta, Lišková, Bültmann, and Burda, 2010). The study of all non-passerine bird families that followed (Lišková and Frynta, 2013) confirmed the significance of blue and yellow colors, with red and purple colors also having a minor effect. More importantly, it revealed that the bird shape, or silhouette, was the strongest predictor of human preferences. However, this study did not include “pattern” as a predictor in the analyses, as the light-contrast differences were only represented by the standard deviation (SD) of lightness. It therefore raised a question about the importance of pattern to human preferences towards birds, as compared to colors and shape.

In this paper, we examined the effects of colors and pattern on human aesthetic preferences of birds. For this purpose, we selected pittas, because they form a monophyletic
group of colorful Old World tropical passerine birds (Moyle, Chesser, Prum, Schikler, and Cracraft, 2006) sharing almost the same shape (silhouette), but they are highly diversified in terms of color and pattern.

Human aesthetic preferences are linked to the evolution of the visual system. As such, the phylogenetic position of humans who belong to the mammalian group of primates should be considered when studying human preferences. The evolutionary biologists reconstructed that the ancestor of all mammals was a small, nocturnal animal (Kemp, 2005). For nocturnal mammals living in the dark, the ability to distinguish objects in achromatic contrast and pattern is of the utmost importance. On the basis of this theory, we can hypothesize that the importance of achromatic vision may be superior to color vision in recent mammals, including primates and humans. The results of human cognitive categorization and color naming as studied by Kay et al. (2010) is in agreement with this. We tested this hypothesis by analyzing the effects of lightness and achromatic pattern on human aesthetic preferences for colorful birds. Simultaneously, we analyzed the effect of basic colors such as red, yellow, green, and blue, asking whether there is some pattern that would confirm the duality of red and yellow (warm colors) on one side and green and blue (cold colors) on the other side. We also investigated the position of the red color, which seems to be salient in the context of evolution of human vision and human color naming and which causes bipolar emotional feelings and arousal.

In short, we tested the effects of (1) lightness and pattern, (2) warm-cool colors continuum, and (3) red color on human aesthetic preferences for pittas. This testing was performed by showing pictures of pittas to human respondents in both full color and grayscale.

Materials and Methods

Selection of species

For the purpose of this study, we selected the morphologically uniform family of Old World passerine birds: the pittas (Pittidae). This group is characterized by flamboyant colors and contrasting patterns that vary considerably among species. Few species are also sexually dichromatic. We examined the aesthetic attractiveness of these birds by presenting a set of 43 pictures to human respondents. The set of pictures included all 32 extant species of pittas (BirdLife International, 2011; we follow the naming of Irestedt, Ohlson, Zuccon, Källersjö, and Ericson, 2006, who recognized three distinct monophyletic groups within the family Pittidae, and proposed generic status to, Hydrornis and Erythropsita formerly belonging to the genus Pitta) and two distinctly colored subspecies (Hydrornis guajana irena, Pitta sordida rosenbergii). In nine distinctly sexually dichromatic species, we included pictures of both sexes (Hydrornis baudii, H. caerulea, H. cyanea, H. elliottii, H. guajana, H. gurneyi, H. nipalensis, H. soror, Pitta schneideri). The colored pictures were adopted from the 8th volume of the Handbook of The Birds of The World (del Hoyo et al., 2003). In order to avoid possible effects of body position, size, and background on rating, the pictures were adjusted with white backgrounds and resized so that the pictured birds were of a similar relative size.

Testing of human preferences

The assessment of human preferences of the depicted birds followed the ranking
method used by Frynta and colleagues (Frynta et al., 2009, 2010, 2011; Lišková and Frynta, 2013; Marešová and Frynta, 2008; Marešová, Krása, and Frynta, 2009; Marešová, Landová, and Frynta, 2009). The respondents were Czech citizens, mostly 19–29 years old. Each person was exposed to one set (i.e., 43 pictures) placed on a table in a random assemblage. Then we asked them, “Please, stack the photographs in an order corresponding to the beauty of the depicted bird, from the most beautiful to the least beautiful one.” The order of the photograph in the pack was then coded by numerals from 1 (the most beautiful one) to 43, further referred to as ranks. The rank-order method maximizes the informative content of the respondents’ judgment by covering the full ordination scale. This ranking method was validated in Frynta et al. (2010), and the preference ranks were highly correlated to scores produced by the Likert scale (5- or 7-point scale). Although no explicit time limit was given, all the respondents performed the task within a few minutes. The pictures were presented to the respondents in a well-lit room during summer daylights. Altogether, we gathered data from 100 respondents (50 males and 50 females). According to self-report, none of the respondents had any form of color blindness. However, the respondents might not have been aware of their condition affecting color vision deficiency. Even if that was the case, the incidence of the most common forms of color blindness is very small, about 7.4% for men and 0.5% for women in European populations (reviewed by Sharpe, Stockman, Jägle, and Nathans, 1999). Thus, the probability of the presence of unrecognized respondents with color deficiency is too small to affect the results treated by robust statistical procedures. To evaluate separately the attractiveness of the pattern of the birds, we repeated the above process with the same set of images set to grayscale. This set was evaluated by another set of 100 Czech respondents (50 males and 50 females).

**Picture processing**

We used a similar procedure in our previous study (Lišková and Frynta, 2013) to characterize the colors present in each picture. Pixel values of the pictures were transformed from the red-green-blue (RGB) colorspace to the so-called hue-saturation-lightness (HSL) colorspace. Hue values are similar to angles on a color wheel, in which certain angles correspond to certain colors. The extraction procedure followed Newsam (2005). In order to avoid dual counting of some pixels (due to the hue angle overlap) and to improve correspondence between color definition and human perception, we adjusted the angle definitions of Newsam (2005) as follows: red <350°, 18°; orange/brown <18°, 45°; yellow <45°, 63°; green <63°, 170°; blue <170°, 270°; and violet-rose <270°, 350°. However, only the basic colors as defined by Kay et al. (2010) were included in further analyses, excluding the orange and violet-rose colors. Moreover, the orange hue as depicted on the actual pictures was mixed with such values of saturation and lightness that it was perceived as “brown” in most of the pictures, which further substantiated the exclusion of the hue; and the violet-rose hue was too rare (very underrepresented) to be analyzed reliably.

We analyzed the portion (in percent) of each such defined color as depicted on the bird (see Figure 1a,b). Although all pixels on the picture, including the background (the area around the object of interest), have their own value for hue, the background pixels were intentionally excluded from the color proportions value analysis using their transparency. This was done using the following method: The color value that was extracted from the picture responded to the number of pixels of each color present in the
picture (including transparent pixels weighted by their transparency) divided by the sum of all non-transparent pixels (the area of the bird “silhouette”). The transparency (A) covered the interval 0–1, 0 being fully transparent, 1 fully visible pixel; the sum of A could be imagined as the number of all pixels the bird covered, compared to the transparent background. The partial transparency of pixels was present only in a minority of pixels at the soft outline of the bird.

**Figure 1.** Colors and edges extractions from the full colored pictures were done using a special software. a) The full-colored, original example of a pitta picture (*Hydrornis elliotii*); b) This picture shows the pitta transformed into fewer pre-defined colors, which were extracted as percentages of total pixels of the given color; c) The last picture illustrates the edges detection, interpretable as the complexity of the pattern.

The values for saturation (S) and lightness (L) covered the interval 0–1. Because human respondents perceive pixels with extreme values of lightness and saturation as black/white and gray (Newsam, 2005), respectively, we defined three additional “colors”: black (L < 0.20), white (L > 0.80), and gray (S < 0.27). Additional variables describing visual quality of each picture that we used to explain human preferences were mean values of S and L, weighted by A, and the standard deviation of S and L, again weighted by A.

The complexity of various patterns as wavelets and spots on the birds’ belly and wings was defined as the portion of contrasting patches on each picture, measured through edge detection, which was processed using the math function of Sobel operator (Sobel, 1978). Each contrasting patch of pixels was detected as an edge and “drawn” on the picture as a light outline—the higher the count of such contrasting patches, the more light outlines there were generated on the picture (see Figure 1c). The final value of the pattern variable, further referred to as “edges” in the text, corresponded to the overall lightness of the generated picture—the lighter the outcome picture, the more complex pattern the bird possessed. In the present picture set, the minimum and maximum values for edges reached from around 0.19 to 0.53.

**Statistical analyses**

In order to quantify and test congruence in species ranking provided by different respondents, we adopted Kendall’s Coefficient of Concordance as implemented in SPSS version 16.0. The contribution of the combinations of the color/greyscale and sex to the variability in ranking species of pittas was examined and visualized in Redundancy
Human preferences for colorful birds

Analysis (RDA) as implemented in CANOCO (ter Braak and Smilauer, 2002). The portion of colored pixels in the tested pictures was square-root arcsin transformed prior to the analyses. Principal Component Analysis (PCA) was performed to visualize the multivariate structure of the data sets and to extract uncorrelated axes for further analyses. Multivariate Analysis of Variance (MANOVA) and General Linear Models (LMs) were applied to test the effects of independent explanatory variables. Full LMs were further reduced according to the Akaike criterion until log-likelihood tests revealed significant comparison between the full and reduced models. We performed most calculations in R and Statistica 6.0.

Ethical note

All respondents agreed to participate in the project voluntarily. Each subject provided an informed consent and additional information about gender and age. The authors declare that the project was approved by the Institutional Review Board (IRB), Faculty of Sciences, Charles University in Prague, approval n.2013/7.

Results

The MANOVA revealed effects of coloration versus grayscale ($\text{Wilks} = 0.4482$, $F_{[42, 155]} = 4.53$, $p < 0.0001$) and gender ($\text{Wilks} = 0.6940$, $F_{42, 155} = 1.63$, $p = 0.02$), but not their interaction ($\text{Wilks} = 0.7231$, $F_{42, 155} = 1.41$, $p = 0.94$) on the ranking of the studied bird species (See Figure 2 for the contribution of particular species to these differences as visualized by RDA plot). When t-tests were performed for each species and set, the gender differences were statistically significant only in six cases. $E$. arcuata, $P$. angolensis, and $P$. reichenowii were more preferred by male respondents and $E$. erythrogaster and $H$. caerulea (male) by female respondents in the colored picture set, whereas $E$. arcuata and $P$. angolensis were more preferred by male respondents and $H$. gurneyi (male) by female respondents in the grayscale picture set. Only two species ($E$. arcuata and $H$. caerulea [male]) remained significant when Bonferonni correction was applied. Because the gender differences were small and involved only 6 (or 2) out of 43 examined species of pittas, we decided to pool the genders in further analyses concerning the means or multivariate axes (PCA) computed from the preference ranks. Both of these methods extract the agreement among respondents and thus further blend the minor effects of gender. The agreement between the respondents was assessed by Kendall’s $W$. It appeared significant ($n = 100$, $df = 42$, $p < 0.001$) in both colored and grayscale picture sets ($Kendall’s W = 0.14$ and 0.21, respectively).

We performed LMs analyzing the factors contributing to the preferences of pitta pictures as evaluated by our respondents. For the colored picture set, we introduced the following explanatory variables to explain the mean preference ranks: lightness and saturation (both $M$ and $SD$), edges, and basic color hues (blue, green, yellow, and red). The initial full-model ($r^2 = 0.76$) revealed a significant contribution of lightness (both $M$ and $SD$), edges, blue, green, and yellow. The final reduced model ($r^2 = 0.75$; see Table 1a and Figure 3) confirmed the effect of mean lightness ($F_{[1, 36]} = 21.98$, $p < 0.0001$), edges ($F_{[1, 36]} = 25.54$, $p < 0.0001$), blue ($F_{[1, 36]} = 19.90$, $p = 0.0001$), green ($F_{[1, 36]} = 27.22$, $p < 0.0001$), and yellow ($F_{[1, 36]} = 7.42$, $p = 0.01$), but $SD$ saturation ($F_{[1, 36]} = 5.74$; $p = 0.02$) was also significant.
Figure 2. The projection of groups of respondents and species of pittas into the first two RDA axes.

Note. Eigenvalues of RDA1 and RDA2 axes are 0.067 and 0.011, respectively. CM - men evaluating colored pictures; CF - women evaluating colored pictures; GM - men evaluating grayscale pictures; GF - women evaluating grayscale pictures. Species names are abbreviated as follows: ane - *Pitta anerythra*, ang - *P. angolensis*, arc - *E. arcuata*, bauM - *H. baudii* male, bauF - *H. baudii* female, bra - *P. brachyura*, caeM - *H. caerulea* male, caeF - *H. caerulea* female, cyaM - *H. cyanea* male, cyaF - *H. cyanea* female, doh - *P. dohertyi*, ele - *P. elegans*, elM - *H. eliotii* male, elf - *H. eliotii* female, fin - *E. erythrogaster*, gra - *E. granatina*, guaM - *H. guajana* male, guaF - *H. guajana* female, ire - *H. guajana* irena, gurM - *H. gurneyi* male, gurF - *H. gurneyi* female, iri - *P. iris*, koc - *E. kochi*, max - *P. maxima*, meg - *P. megargyrrha*, mol - *P. moluccensis*, nipM - *H. nipalensis* male, nipF - *H. nipalensis* female, nym - *P. nympha*, oat - *H. oatesi*, pha - *H. phayrei*, rei - *P. reichenowi*, schM - *P. schneideri* male, schF - *P. schneideri* female, sor - *P. sordida*, ros - *P. sordida* rosenbergii, sorM - *H. soror* male, sorF - *H. soror* female, ste - *P. steerii*, sup - *P. superba*, uss - *P. ussherii*, ven - *E. venusta*, ver - *P. versicolor*.

When evaluating the mean preference ranks of the grayscale pictures, those explanatory variables involving coloration (saturation, blue, green, yellow, red) were not applicable and thus we performed LMs including only M and SD lightness and edges. Both full- and reduced models ($r^2 = 0.55$ and 0.54, respectively; see Table 1b and Figure 3)
revealed the effects of edges (the reduced model: \(F[1,40] = 39.79; p < 0.0001\)) and mean lightness (the reduced model: \(F[1,40] = 6.25, p = 0.02\)).

### Table 1. ANOVA tables and coefficients of General Linear Models (LMs)

**a) Response: Mean preference ranks of the colored set**

| ANOVA          | Coefficients |
|----------------|--------------|
|                | Estimate     | Std. Error | t   | p    |
| (Intercept)    | 0.43         | 0.17       | 2.51| 0.02 |
| Mean L         | 0.75         | 0.26       | 2.94| 0.01 |
| Edges          | -0.18        | 0.05       | -3.55| 0.001|
| Std S          | -0.69        | 0.39       | -1.78| 0.08 |
| Blue           | -0.48        | 0.08       | -6.16| <0.0001|
| Green          | -0.18        | 0.07       | -2.70| 0.01 |
| Yellow         | -0.32        | 0.12       | -2.73| 0.01 |

**b) Response: Mean preference ranks of the grayscaled set**

| ANOVA          | Coefficients |
|----------------|--------------|
|                | Estimate     | Std. Error | t   | p    |
| (Intercept)    | 0.33         | 0.15       | 2.18| 0.04 |
| Edges          | -0.39        | 0.07       | -5.73| <0.0001|
| Mean L         | -0.67        | 0.27       | -2.50| 0.02 |

**c) Response: PC1 extracted from the grayscaled set preference ranks**

| ANOVA          | Coefficients |
|----------------|--------------|
|                | Estimate     | Std. Error | t   | p    |
| (Intercept)    | 1.02         | 0.99       | 1.02| 0.31 |
| Edges          | 2.41         | 0.36       | 6.70| <0.0001|
| Mean L         | 3.56         | 1.30       | 2.74| 0.01 |
| Std L          | 4.09         | 2.93       | 1.40| 0.17 |

**d) Response: PC2 extracted from the grayscaled set preference ranks**

| ANOVA          | Coefficients |
|----------------|--------------|
|                | Estimate     | Std. Error | t   | p    |
| (Intercept)    | -3.45        | 0.88       | -3.91| 0.0004|
| Mean L         | 11.64        | 1.15       | 10.12| <0.0001|
| Std L          | -10.68       | 2.59       | -4.13| <0.0001|
| Edges          | -0.71        | 0.32       | -2.24| 0.03 |

**e) Response: PC1 extracted from the colored set preference ranks**

| ANOVA          | Coefficients |
|----------------|--------------|
|                | Estimate     | Std. Error | t   | p    |
| (Intercept)    | -1.72        | 0.49       | -3.49| 0.001|
| PC2 greyscale  | -0.39        | 0.10       | -3.95| 0.0004|
| Std S          | 5.99         | 1.95       | 3.07| 0.004|
| Mean S         | -2.20        | 0.94       | -2.34| 0.03 |
| Blue           | 2.64         | 0.40       | 6.57| <0.0001|
| Green          | 1.28         | 0.35       | 3.68| <0.0001|
| Yellow         | 1.04         | 0.48       | 2.20| 0.03 |
| Red            | 0.99         | 0.51       | 1.96| 0.06 |

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Figure 3. Effect sizes as revealed by General Linear Models (LMs)

Because the respondents’ discrimination may reflect more than one axis (set of characters), we extracted multiple principal component axes from the preference rankings. The first three principal axes explained 28.4%, 13.7%, and 7.7% of the total variance of the colored picture set, respectively. The corresponding values for the grayscale picture set were 31.0%, 16.0%, and 8.4%. We further analyzed these components and found that the first and second components of both sets are mutually closely correlated (PC1 color vs PC2 grayscale: $r^2 = 0.64$, $p < 0.0001$; PC2 color vs PC1 grayscale: $r^2 = 0.83$, $p < 0.0001$) and thus probably reflect a similar set of traits used by the respondents as a guide for ranking.

In order to identify these putative traits, we analyzed the first two principal axes by LMs in a similar way to the mean values of preference ranks as described above. First, we analyzed PCs derived from the grayscale picture set that represents a simpler model. PC1 of the grayscale set ($r^2 = 0.68$; see Table 1c) was explained by edges ($F[1, 39] = 72.5$, $p < 0.0001$) and mean lightness ($F[1, 39] = 8.45$, $p = 0.01$). PC2 of the grayscale set ($r^2 = 0.75$; see Table 1d) was explained by mean lightness ($F[1, 39] = 83.06$, $p < 0.0001$), SD lightness ($F[1, 39] = 29.02$, $p < 0.0001$), and edges ($F[1, 39] = 5.01$, $p = 0.03$). Next, we analyzed PC1 derived from the color set and included PC2 derived from the grayscale set as a predictor instead of the edges and lightness, which already contributed to this variable. The resulting LM ($r^2 = 0.87$; see Table 1e) revealed that besides the fundamental contribution of PC2 grayscale ($F[1, 35] = 167.77$, $p < 0.0001$), highly significant and positive effects of
Human preferences for colorful birds

blue ($F[1, 35] = 26.16, p < 0.0001$) and green ($F[1, 35] = 17.23, p < 0.0001$) colors on human preferences of colored pictures were also present.

Discussion

We analyzed the effects of colors and achromatic components ($M$ and $SD$ of lightness, pattern) on human preferences for colorful birds of the family Pittidae. Surprisingly, the respondents ranked the birds’ aesthetics similarly in both the full colored and grayscale picture sets. More detailed analysis of the preference ranks revealed that in both cases, pattern and lightness components affected human preferences more than the analyzed color hues. Blue and green hues were the only colors that had minor, yet significant, effects on human aesthetic ranking of the colored birds picture set.

One would expect that the respondents are able to rank color pictures more easily and reliably than the grayscale ones. During the testing procedure, the respondents showed higher willingness to rank the colored pictures as these apparently presented a more appealing and motivating challenge. However, our results show that the Kendall coefficient of agreement was slightly higher among the respondents ranking the grayscale than among those ranking the colored set. This finding may be explained by the distracting effect of colors on the respondents. It was shown in both monkeys (Saito et al., 2005) and humans (Morgan, Adam, and Mollon, 1992; Saito, Mikami, Hosokawa, and Hasegawa, 2006) that dichromats solved tasks involving detection of objects camouflaged in red pattern with a higher success rate than trichromats.

In our study, the mean ranks of pictures resulting from the grayscale set were slightly, but significantly, correlated with those obtained from the color test ($r^2 = 0.10, p = 0.04$). Nevertheless, multivariate analyses clearly revealed that the same two main axes are behind the ranking of both sets. We extracted the first two main principal components (PC, multivariate orthogonal axes) from the ranking results of both color and grayscale sets. The colored set PC1 closely correlated with the grayscale set PC2 and vice versa (grayscale PC1 correlated with color PC2). Such close mutual correlation of the color and grayscale axes suggests that principal cues determining ranking of the color pictures are also present in the grayscale pictures possessing only achromatic components. Thus, these principal cues cannot be composed of chromatic colors. The fundamental role of achromatic components was further supported by the GLM analyses of the PC axes. These axes may be interpreted mainly as the pattern complexity for grayscale PC1/color PC2 and overall lightness for grayscale PC2/color PC1. The presence of the chromatic component in the color pictures, however, affects the priority of the axes adopted for aesthetic ranking; it induces a switch from primary use of the pattern axis to the lightness one. In short, people tend to rank grayscale pictures according to pattern, while they rank color pictures according to overall lightness.

In this regard, it is useful to review the role of chromatic and achromatic (shape and pattern) information in solving various human cognitive tasks. In the study of Mullen and Beaudot (2002), color vision performed worse than luminance vision in a shape discrimination task. Shape has also been found to play a primary role in object recognition (electrophysiologically measured) when human respondents were instructed to pay attention to various objects or colors on a computer screen (Proverbio, Burco, del Zotto, and Zani, 2004). They were able to discriminate colors faster if these were associated with
Human preferences for colorful birds

canonical shapes (e.g., a yellow chicken was recognized faster than a yellow piglet), but not vice versa; canonical colors did not help the respondents to recognize shapes faster. However, when naming objects is the task, canonic chroma helps to name the objects faster (Therriault, Yaxley, and Zwaan, 2009), and in some cases, chroma helps humans to recognize objects faster and to remember them better (Spence, Wong, Rusan, and Rastegar, 2006; Wichmann, Sharpe, and Gegenfurtner, 2002). Whenever the shape of an object is unavailable for some reason, chromatic information helps in the object recognition (Liebe, Fischer, Logothetis, and Rainer, 2009; Steeves et al., 2004; Yip and Sinha, 2002), especially when the respondents already possess “color knowledge” of particular objects stored in long-term memory (Mapelli and Behrmann, 1997). In ultra-rapid recognition tasks, however, both humans and monkeys are able to categorize an animal or food object on flashing pictures regardless of the presence of chromatic information (Delorme, Richard, and Fabre-Thorpe, 2000). Moreover, humans are able to categorize the objects even if presented in a grayscale at a very low luminance contrast (Macé, Thorpe, and Fabre-Thorpe, 2005). Similar rapid-presentation experiments show that humans’ recognition of sketched shapes of objects is as good as their recognition of high quality colorful photographs (Biederman and Ju, 1988). Thus, shape and grayscale pattern provide primary information for human perception, while color contributes to cognitive interpretation and memory processing of an already recognized object (picture).

The ranking procedure in our experiment instructed the respondents to arrange the pictures according to a gradient of aesthetic preferences. The objective of the testing was not categorization of the objects and the respondents were not instructed to intentionally do so. However, it has been previously shown that in a similar experiment using the same testing method, the respondents still categorized the ranked subjects (snakes; Landová, Marešová, Šimková, Cikánová, and Frynta, 2012; Marešová, Landová, et al., 2009). This resembles the task recognized as unsupervised human categorization by some authors (Pothos and Chater, 2002; Pothos and Close, 2008). Although the respondents were mainly students of biology, the majority of them did not recognize that the tested birds belonged to the family Pittidae and none of the respondents were able to distinguish the particular species. This may be why the role of chroma was not so prominent in the ranking of aesthetics of birds, as the respondents did not try to intentionally categorize the species nor did they need to recognize them using long-term memory references.

Our results showed that human respondents rank the attractiveness of colorful birds mainly on the basis of lightness and pattern. This finding is in agreement with the model of color categorization and naming of Kay et al. (2010), which finds “black” and “white” colors as the first to appear in lingual color terms construction. In other words, the separation of black and white can be understood as the separation of dark and light colors (as perceived in luminance and partially also chromatic contrast), which may in fact correspond to the distinction along the axis of overall perceived lightness.

In this study, the only chromatic colors to affect human preferences towards the birds depicted in color were blue and green. This implies the relevance of the division of chromatic spectrum into warm and cool colors, with warm colors having no effect on human aesthetic preferences towards pittas. Blue and green hues are often reported to positively affect the emotional feelings of humans who associate both of the hues together with peace and calmness (Ball, 1965; Kaya and Epps, 2004). Blue birds have been consistently highly ranked within various contexts (in various bird groups, tested
Human preferences for colorful birds

independently): blue-and-white flycatcher, indigo-banded kingfisher, hyacinth macaw, and Indian roller (Frynta et al., 2009, 2010; Lišková and Frynta, 2013). The preference for blue and green color has also been found in non-human primates. Chimpanzees and gorillas preferred to manipulate blue and green objects over red ones (Wells, McDonald, and Ringland, 2008), and macaques were also reported to prefer blue colors (Humphrey, 1972). Sharing of this preference for the color blue with our monkey and ape relatives suggests that this character is deeply rooted in the ancestry of humans.

We found no effect of the color red on human aesthetic preferences of pittas. This may be explained by a relatively short history of the color’s recognition in primates. The cones sensitive to red light have evolved in a common ancestor of Old World monkeys and apes, i.e., relatively recently when compared to those sensitive to green and blue light. It is recently a matter of discussion whether trichromatic primates have any advantage over the dichromatic ones. Traditional views supported by many papers say that trichromatic primates are quicker in foraging for red ripe fruits (e.g., Osorio and Vorobyev, 1996; Surridge et al., 2003) or young leaves (Dominy and Lucas, 2001; Lucas, Darvell, Lee, Yuen, and Choong, 1998). However, a recent study by Hiramatsu et al. (2008) found no advantage of trichromats in the recognition of food in black-handed spider monkeys. They show that luminance contrast was the main determinant of the variation of foraging efficiency. Moreover, the uneven distribution of L, M, and S cone sensitivities in primates (as opposed to even distribution, optimal for maximal color discrimination, found in non-mammalian trichromats such as birds or bees; Kremers, 2005; Osorio and Vorobyev, 2005) may also point to the importance of luminance contrast discrimination, because separate L and M cones have the potential to corrupt luminance signals (Osorio, Ruderman, and Cronin, 1998).

Phylogenetic studies show that trichromatism in primates evolved most likely in the context of foraging performance (Fernandez and Morris, 2007). Once evolved, the ability to see the color red gained its importance in the selection of red-colored sexual traits and communication (Waitt et al., 2003; Waitt, Gerald, Little, and Kraiselburd, 2006). Changizi, Zhang, and Shimojo (2006) pointed out that primates with trichromatic vision tend to have bare faces and that bare skin modulations serve as a signaling on the uncovered body parts. The red color signalization then may facilitate either approach or avoidance behavior, depending on the context (Meier, D’Agostino, Elliot, Maier, and Wilkowski, 2012). In some primates, the red color of the chest and genitals signals sexual receptivity (Deschner, Heistermann, Hodges, and Boesch, 2004; Waitt et al., 2006) and increases sexual receptivity in watching males (Bielt, Girolami, and Jowell, 1989). The effect of red on sexual signaling and romance has also been reported in many human studies, showing that respondents wearing red or holding red items were perceived as more attractive by the opposite gender (e.g., Elliot and Niesta, 2008; Elliot et al., 2010; Guèguen, 2012; Lin, 2014; Pazda, Elliot, and Greitemeyer, 2012; Roberts, Owen, and Havlicek, 2010; Schwarz and Singer, 2013; but see Johns, Hargrave, and Newton-Fisher, 2012), and this effect seems to be universal (Elliot, Tracy, Pazda, and Beall, 2013).

In opposition to this, the color red can signal threat and danger. For example, in male baboons, a red face signals dominance and a threat to potential opponents (Setchell and Jean Wickings, 2005) and a red-colored chest is associated with an avoidance (or withdrawal) response in geladas (Bergman, Ho, and Beehner, 2009). In humans, facial red color signals anger (Fetterman, Robinson, Gordon, and Elliot, 2011; Young, Elliot,
Human preferences for colorful birds

Feltman, and Ambady, 2013), and is reported to facilitate avoidance behavior in human respondents when presented in the context of competition (Meier et al., 2012). Thus, instead of having a specific effect, the color red seems to have a strong, context-dependent motivational effect on human perceivers. Buechner, Maier, Lichtenfeld, and Schwarz (2014) showed that red intensifies attention to goal-relevant stimuli. It is a “signal of relevance which carries the message that a present stimulus is important and worthy of attention” (Buechner et al., 2014, p. 1). Only after this message is received, the information is processed according to the specific context to facilitate either the approach or avoidance behavior.

Although the color red facilitates attentional adhesion in human respondents to important stimuli such as human facial expressions, it has no relevance on perceiving small passerine birds. This may explain why red had no effect on our respondents’ rating of perceived “beauty” of the birds. However, in a previous study concerning the perception of attractiveness of king snakes (Landová et al., 2012), the color red was perceived as attractive by human respondents. This may be explained by attentional adhesion to conspicuous species with aposematic coloration, relevant to human survival, which affects both rating of attractiveness and perceived dangerousness of the snakes (although harmless, king snakes of the genus Lampropeltis are Batesian mimics of the dangerous and deadly poisonous snakes of the genus Micrurus from the family Elapidae). Because the respondents noticed the potentially dangerous animal before it attacked, it could result in a pleasant emotion, which in turn could reflect onto the aesthetic rating of the snakes. In a different study by Prokop and Fančovičová (2012), human respondents preferred red fruits over green or brown ones. This preference could also be explained by the attentional adhesion effect of the color red, as preferring ripe red fruits is in agreement with the foraging hypothesis of the evolution of primate trichromatic vision (Fernandez and Morris, 2007).

The color red is the most ambiguous one, often eliciting both positive and negative emotions and associations (Kaya and Epps, 2004; Wang, Shu, and Mo, 2014), but other colors are perceived differently in various contexts as well. For example, respondents who prefer blue reported that they would prefer this color on clothing but not on furniture (for a review, see Taft, 1997). The color blue is the least ambiguous, preferred by most respondents in many studies (Dittmar, 2000; Hemphill, 1996; Madden, Hewett, and Roth, 2000; Saito, 1994). Still, it can also be sometimes assigned with a negative feeling such as depression, sadness, and loneliness (Kaya and Epps, 2004). The saying that one “feels blue” may not only be associated with depression, but can also be linked to an actual signaling of a person’s health, as a bluish tint of skin can signal a bad health condition of low-level blood oxygenation (Re, Whitehead, Xiao, and Perrett, 2011). It is possible that animals or natural shapes (as opposed to neutral or novel objects), which represent evolutionarily important stimuli for human respondents due to the coevolutionary history of animals and humans, can trigger different emotional reactions than abstract and arbitrary shapes with no connection to human evolution. It is thus very important to study both abstract and natural stimuli to gain sound insight into human visual perception.

Although there is immense evidence for the importance of colors in many aspects of human life, such as emotional affection, easier object categorization (assignment into distinctive cognitive groups), arousal, or selective attention, we found only a small effect of colors on human aesthetic preferences for birds. The only colors that had minor effects
were blue and green. The main factors affecting human preferences were the pattern and overall lightness. This finding emphasizes the key role of the luminance contrast discrimination, the importance of which is shared ancestrally within dichromatic primates.

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References

Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
Ball, V. K. (1965). The aesthetics of color: A review of fifty years of experimentation. The Journal of Aesthetics and Art Criticism, 23, 441–452.
Bennett, P., and Owens, I. (2002). Evolutionary ecology of birds: Life histories, mating systems, and extinction. Oxford: Oxford University Press.
Bergman, T. J., Ho, L., and Beehner, J. C. (2009). Chest color and social status in male geladas (Theropithecus gelada). International Journal of Primatology, 30, 791–806.
Berlin, B., and Kay, P. (1969). Basic color terms. Berkeley: University of California Press.
Biederman, I., and Ju, G. (1988). Surface- versus edge-based determinants of visual recognition. Cognitive Psychology, 20, 38–64.
Bielert, C., Girolami, L., and Jowell, S. (1989). An experimental examination of the colour component in visually mediated sexual arousal of the male chacma baboon (Papio ursinus). Journal of Zoology, 219, 569–579.
BirdLife International (2011). The BirdLife checklist of the birds of the world, with conservation status and taxonomic sources. Version 4. Downloaded from http://www.birdlife.info/im/species/checklist.zip [.xls zipped 1 MB].
Bowmaker, J. K. (2008). Evolution of vertebrate visual pigments. Vision Research, 48, 2022–2041.
Buechner, V. L., Maier, M. A., Lichtenfeld, S., and Schwarz, S. (2014). Red - Take a closer look. PLOS ONE, 9, e108111.
Changizi, M. A., Zhang, Q., and Shimojo, S. (2006). Bare skin, blood and the evolution of primate colour vision. Biology Letters, 2, 217–221.
Crozier, W. R. (1997). The psychology of colour preferences. Surface Coatings International, 80, 577–585.
del Hoyo, J., Elliott, A., and Christie, D. (2003). Handbook of the birds of the world. Vol. 8. Broadbills to tapaculos. Barcelona: Lynx edicions.
Human preferences for colorful birds

Delorme, A., Richard, G., and Fabre-Thorpe, M. (2000). Ultra-rapid categorisation of natural scenes does not rely on colour cues: A study in monkeys and humans. *Vision Research, 40*, 2187–2200.

Deschner, T., Heistermann, M., Hodges, K., and Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior, 46*, 204–215.

Dittmar, M. (2000). Changing colour preferences with ageing: A comparative study on younger and older native Germans aged 19-90 years. *Gerontology, 47*, 219–226.

Dominy, N. J., and Lucas, P. W. (2001). Ecological importance of trichromatic vision to primates. *Nature, 410*, 363–366.

Elliot, A. J., and Maier, M. (2007). Color and psychological functioning. *Current Directions in Psychological Science, 16*, 250–254.

Elliot, A. J., Maier, M. A., Moller, A. C., Friedman, R., and Meinhardt, J. (2007). Color and psychological functioning: The effect of red on performance attainment. *Journal of Experimental Psychology, 136*, 154–168.

Elliot, A. J., and Niesta, D. (2008). Romantic red: Red enhances men’s attraction to women. *Journal of personality and social psychology, 95*, 1150–1164.

Elliot, A. J., Niesta, D., Greitemeyer, T., Lichtenfeld, S., Gramzow, R. H., Maier, M. A., and Liu, H. (2010). Red, rank, and romance in women viewing men. *Journal of Experimental Psychology: General, 139*, 399–417.

Elliot, A. J., Tracy, J. L., Pazda, A. D., and Beall, A. T. (2013). Red enhances women’s attractiveness to men: First evidence suggesting universality. *Journal of Experimental Social Psychology, 49*, 165–168.

Fernandez, A. A., and Morris, M. R. (2007). Sexual selection and trichromatic color vision in primates: Statistical support for the preexisting bias hypothesis. *The American Naturalist, 170*, 10–20.

Fetterman, A. K., Robinson, M. D., Gordon, R. D., and Elliot, A. J. (2011). Anger as seeing red: Perceptual sources of evidence. *Social Psychological and Personality Science, 2*, 311-316.

Frynta, D., Lišková, S., Bültmann, S., and Burda, H. (2010). Being attractive brings advantages: The case of parrot species in captivity. *PLOS ONE, 5*, e12568.

Frynta, D., Marešová, J., Landová, E., Lišková, S., Šimková, O., Tichá, I., . . . Fuchs, R. (2009). Are animals in zoos rather conspicuous than endangered? In A. M. Columbus and L. Kuznetsov (Eds.), *Endangered species: New research* (pp. 299–341). New York: Nova Science Publishers.

Frynta, D., Marešová, J., Řeháková-Petrů, M., Škliba, J., Šembera, R., and Kráša, A. (2011). Crosscultural agreement in perception of animal beauty: Boid snakes viewed by people from three continents. *Human Ecology, 39*, 829–834.

Frynta, D., Šimková, O., Lišková, S., and Landová, E. (2013). Mammalian collection on Noah’s Ark: The effects of beauty, brain and body size. *PLOS ONE, 8*, e63110.

Gao, X.-P., Xin, J. H., Sato, T., Hansuebsai, A., Scalzo, M., Kajiwara, K., . . . Billger, M. (2007). Analysis of cross-cultural color emotion. *Color Research and Application, 32*, 223–229.

Gorn, G. J., Chattopadhyay, A., Yi, T., and Dahl, D. W. (1997). Effects of color as an executional cue in advertising: They’re in the shade. *Management Science, 43*, 1387–1400.
Guéguen, N. (2012). Color and women attractiveness: When red clothed women are perceived to have more intense sexual intent. The Journal of Social Psychology, 152, 261–265.

Hart, N., Bailes, H., Vorobyev, M., Marshall, N. J., and Collin, S. (2008). Visual ecology of the Australian lungfish (Neoceratodus forsteri). BMC Ecology, 8, 21.

Heesy, Ch. P., and Hall, M. I. (2010). The nocturnal bottleneck and the evolution of mammalian vision. Brain, Behavior and Evolution, 75, 195–203.

Hemphill, M. (1996). A note on adults’ color-emotion associations. The Journal of Genetic Psychology, 157, 275–280.

Hill, R. A., and Barton, R. A. (2005). Psychology: Red enhances human performance in contests. Nature, 435, 293.

Hiramatsu, C., Melin, A. D., Aureli, F., Schaffner, C. M., Vorobyev, M., Matsumoto, Y., and Kawamura, S. (2008). Importance of achromatic contrast in short-range fruit foraging of primates. PLOS ONE, 3, e3356.

Humphrey, N. K. (1972). ‘Interest’ and ‘pleasure’: Two determinants of a monkey’s visual preferences. Perception, 1, 395–416.

Ioan, S., Sandulache, M., Avramescu, S., Ilie, A., Neacsu, A., Zagrean, L., and Moldavan, M. (2007). Red is a distractor for men in competition. Evolution and Human Behavior, 28, 285–293.

Irestedt, M., Ohlson, J. I., Zuccon, D., Källersjö, M., and Ericson, P. G. (2006) Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zoologica Scripta, 35, 567–580.

Jacobs, G. H. (2009). Evolution of colour vision in mammals. Philosophical Transactions of the Royal Society B: Biological Sciences, 364, 2957–2967.

Johns, S. E., Hargrave, L. A., and Newton-Fisher, N. E. (2012). Red is not a proxy signal for female genitalia in humans. PLOS ONE, 7, e34669.

Kay, P., Berlin, B., Maffi, L., Merrifield, W. R., and Cook, R. (2010). The world color survey. Stanford: Center for the Study of Language and Inf.

Kaya N., and Epps, H. (2004). Relationship between color and emotion: A study of college students. College Student Journal, 38, 396–405.

Kemp, T. S. (2005). The origin and evolution of mammals. Oxford, UK: Oxford University Press.

Kremers, J. (Ed.). (2005). The primate visual system: A comparative approach. New York: John Wiley and Sons, Ltd.

Landová, E., Marešová, J., Šimková, O., Cikánová, V., and Frynta, D. (2012). Human responses to live snakes and their photographs: Evaluation of beauty and fear of the king snakes. Journal of Environmental Psychology, 32, 69–77.

Liebe, S., Fischer, E., Logothetis, N. K., and Rainer, G. (2009). Color and shape interactions in the recognition of natural scenes by human and monkey observers. Journal of Vision, 9, 1–16.

Lin, H. (2014). Red-colored products enhance the attractiveness of women. Displays, 35, 202–205.

Lišková, S., and Frynta, D. (2013). What determines bird beauty in human eyes? Anthrozoos: A Multidisciplinary Journal of the Interactions of People and Animals, 26, 27–41.
Human preferences for colorful birds

Lucas, P. W., Darvell, B. W., Lee, P. K. D., Yuen, T. D. B., and Choong, M. F. (1998). Colour cues for leaf food selection by long-tailed macaques (Macaca fascicularis) with a new suggestion for the evolution of trichromatic colour vision. Folia Primatologica, 69, 139–154.

Macé, M. J. M., Thorpe, S. J., and Fabre-Thorpe, M. (2005). Rapid categorization of achromatic natural scenes: How robust at very low contrasts? European Journal of Neuroscience, 21, 2007–2018.

Madden, T. J., Hewett, K., and Roth, M. S. (2000). Managing images in different cultures: A cross-national study of color meanings and preferences. Journal of International Marketing, 8, 90–107.

Mahnke, F. H. (1996). Color, environmental and human response. New York: Van Nostrand Reinhold.

Manav, B. (2007). Color-emotion associations and color preferences: A case study for residences. Color Research and Application, 32, 144–150.

Mapelli, D., and Behrmann, M. (1997). The role of color in object recognition: Evidence from visual agnosia. Neurocase, 3, 237–247.

Marešová, J., and Frynta, D. (2008). Noah’s Ark is full of common species attractive to humans: The case of boid snakes in zoos. Ecological Economics, 64, 554–558.

Marešová, J., Krása, A., and Frynta, D. (2009). We all appreciate the same animals: Cross-cultural comparison of human aesthetic preferences for snake species in Papua New Guinea and Europe. Ethology, 115, 297–300.

Marešová, J., Landová, E., and Frynta, D. (2009). What makes some species of milk snakes more attractive to humans than others? Theory in Biosciences, 128, 227–235.

Martin, R. D., and Ross, C. F. (2005). The evolutionary and ecological context of primate vision. In J. Kremers (Ed.), The primate visual system: A comparative approach (pp 1–36). New York: John Wiley and Sons.

Meier, B. P., D’Agostino, P. R., Elliot, A. J., Maier, M. A., and Wilkowski, B. M. (2012). Color in context: Psychological context moderates the influence of red on approach-and avoidance-motivated behavior. PLOS ONE, 7, e40333.

Metrick, A., and Weitzman, M. L. (1996). Patterns of behaviour in endangered species preservation. Land Economics, 72, 1–16.

Morgan, M. J., Adam, A., and Mollon, J. D. (1992). Dichromats detect colour-camouflaged objects that are not detected by trichromats. Proceedings of the Royal Society of London. Series B: Biological Sciences, 248, 291–295.

Moyle, R. G., Chesser, R. T., Prum, R. O., Schikler, P., and Cracraft, J. (2006). Phylogeny and evolutionary history of Old World suboscine birds (Aves: Eurylaimides). American Museum Novitates, 3544, 1–22.

Mullen, K. T., and Beaudot, W. H. (2002). Comparison of color and luminance vision on a global shape discrimination task. Vision Research, 42, 565–576.

Newsam, S. (2005). Seeing and reading red: Hue and color-word correlation in images and attendant text on the WWW. In Proceedings of The 6th International Workshop on Multimedia Data Mining: Mining Integrated Media and Complex Data, 101–106. New York: ACM.

Osorio, D., Ruderman, D. L., and Cronin, T. W. (1998). Estimation of errors in luminance signals encoded by primate retina resulting from sampling of natural images with red and green cones. Journal of the Optical Society of America A, 15, 16–22.
Osorio, D., and Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263, 593–599.

Osorio, D., and Vorobyev, M. (2005). Photoreceptor spectral sensitivities in terrestrial animals: Adaptations for luminance and colour vision. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1745–1752.

Pazda, A. D., Elliot, A. J., and Greitemeyer, T. (2012). Sexy red: Perceived sexual receptivity mediates the red-attraction relation in men viewing woman. *Journal of Experimental Social Psychology*, 48, 787–790.

Pothos, E. M., and Chater, N. (2002). A simplicity principle in unsupervised human categorization. *Cognitive Science*, 26, 303–343.

Pothos, E. M., and Close, J. (2008). One or two dimensions in spontaneous classification: A simplicity approach. *Cognition*, 107, 581–602.

Prokop, P., and Fančovičová, J. (2012). Beautiful fruits taste good: The aesthetic influences of fruit preferences in humans. *Anthropologischer Anzeiger*, 69, 71–83.

Proverbio, A. M., Burco, F., del Zotto, M., and Zani, A. (2004). Blue piglets? Electrophysiological evidence for the primacy of shape over color in object recognition. *Cognitive Brain Research*, 18, 288–300.

Re, D. E., Whitehead, R. D., Xiao, D., and Perrett, D. I. (2011). Oxygenated-blood colour change thresholds for perceived facial redness, health, and attractiveness. *PLOS ONE*, 6, e17859.

Roberts, S. C., Owen, R. C., and Havlicek, J. (2010). Distinguishing between perceiver and wearer effects in clothing color-associated attributions. *Evolutionary Psychology: an International Journal of Evolutionary Approaches to Psychology and Behavior*, 8, 350–364.

Saito, M. (1994). A cross-cultural study on color preference in three Asian cities: Comparison between Tokyo, Taipei and Tianjin. *Japanese Psychological Research*, 36, 219–232.

Saito, M. (1996). Comparative studies on color preference in Japan and other Asian regions, with special emphasis on the preference for white. *Color Research and Application*, 21, 35–49.

Saito, A., Mikami, A., Hosokawa, T., and Hasegawa, T. (2006). Advantage of dichromats over trichromats in discrimination of color-camouflaged stimuli in humans 1, 2. *Perceptual and Motor Skills*, 102, 3–12.

Saito, A., Mikami, A., Kawamura, S., Ueno, Y., Hiramatsu, C., Widayati, K. A., . . . Hasegawa, T. (2005). Advantage of dichromats over trichromats in discrimination of color-camouflaged stimuli in nonhuman primates. *American Journal of Primatology*, 67, 425–436.

Schwarz, S., and Singer, M. (2013). Romantic red revisited: Red enhances men’s attraction to young, but not menopausal women. *Journal of Experimental Social Psychology*, 49, 161–164.

Setchell, J. M., and Jean Wickings, E. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, 111, 25–50.

Setchell, J. M., Jean Wickings, E., and Knapp, L. A. (2006). Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proceedings of the Royal Society B: Biological Sciences*, 273, 2395–2400.
Sharpe, L. T., Stockman, A., Jägle, H., and Nathans, J. (1999) Opsin genes, cone photopigments, color vision, and color blindness. In K. R. Gegenfurtner and L. T. Sharpe (Eds.), Color vision: From genes to perception (pp. 3–51). Cambridge: Cambridge University Press.

Sobel, I. (1978). Neighbourhood coding of binary images fast contour following and general array binary processing. Computer Graphics and Image Processing, 8, 127–135.

Spence, I., Wong, P., Rusan, M., and Rastegar, N. (2006). How color enhances visual memory for natural scenes. Psychological Science, 17, 1–6.

Steeves, J. K., Humphrey, G. K., Culham, J. C., Menon, R. S., Milner, A. D., and Goodale, M. A. (2004). Behavioral and neuroimaging evidence for a contribution of color and texture information to scene classification in a patient with visual form agnosia. Journal of Cognitive Neuroscience, 16, 955–965.

Surridge, A. K., Osorio, D., and Mundy, N. I. (2003). Evolution and selection of trichromatic vision in primates. Trends in Ecology and Evolution, 18, 198–205.

Taft, C. (1997). Color meaning and context: Comparisons of semantic ratings of colors on samples and objects. Color Research and Application, 22, 40–50.

ter Braak, C. J. F., and Smilauer, P. (2002). CANOCO reference manual and CanoDraw for Windows user’s guide: Software for canonical community ordination (Version version 4.5) [Computer software]. New York: Microcomputer Power, Ithaca.

Therriault, D. J., Yaxley, R. H., and Zwaan, R. A. (2009). The role of color diagnosticity in object recognition and representation. Cognitive Processing, 10, 335–342.

Waitt, C., Gerald, M. S., Little, A. C., and Kraislcurb, E. (2006). Selective attention toward female secondary sexual color in male rhesus macaques. American Journal of Primatology, 68, 738–744.

Waitt, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M., and Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. Proceedings of the Royal Society of London. Series B: Biological Sciences, 270, S144–S146.

Wang, T., Shu, S., and Mo, L. (2014). Blue or red? The effects of colour on the emotions of Chinese people. Asian Journal of Social Psychology, 17, 152–158.

Wells, D. L., McDonald, C. L., and Ringland, J. E. (2008). Color preferences in gorillas (Gorilla gorilla gorilla) and chimpanzees (Pan troglodytes). Journal of Comparative Psychology, 122, 213–219.

Whorf, B. L., and Carroll, J. B. (1956). Language, thought, and reality: Selected writings of Benjamin Lee Whorf: Vol. 5. Cambridge: MIT Press.

Wichmann, F. A., Sharpe, L. T., and Gegenfurtner, K. R. (2002). The contributions of color to recognition memory for natural scenes. Journal of Experimental Psychology - Learning Memory and Cognition, 28, 509–520.

Wilson, G. D. (1966). Arousal properties of red versus green. Perceptual and Motor Skills, 23, 947–949.

Wolfrom, S., and Case, G. (2000). The effects of sound and colour on responses to a computer game. Interacting with Computers, 13, 183–192.

Yip, A. W., and Sinha, P. (2002). Contribution of color to face recognition. Perception, 31, 995–1004.
Young, S. G., Elliot, A. J., Feltman, R., and Ambady, N. (2013). Red enhances the processing of facial expressions of anger. *Emotion, 13*, 380.
Zhao, H., Rossiter, S. J., Teeling, E. C., Li, C., Cotton, J. A., and Zhang, S. (2009). The evolution of color vision in nocturnal mammals. *Proceedings of the National Academy of Sciences, 106*, 8980–8985.