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ORIGINAL ARTICLE

# Assessing male gelada chest patches: color measurement and physiological mechanisms

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## Abstract

Selective pressures have favored conspicuous coloration across a wide variety of taxa. A particularly striking example of conspicuous coloration is the brilliant red chest patch of male geladas (*Theropithecus gelada*), a species of cercopithecine monkey found in the high-altitude regions of Ethiopia. Previous research found that gelada chest patch redness increases with age (adult vs subadult), social status ("leader" vs non-leader), and mating opportunities (number of adult females), but the mechanism mediating changes in redness has not yet been examined. First, we validated and compared multiple color measurement methods (Adobe Photoshop, micaToolbox designed for use with ImageJ, and a subjective measure using the human eye). Second, we demonstrated that chest patch redness is positively associated with high-intensity physical activity, the application of a heat pack directly to the chest skin, and higher chest skin surface temperatures. Together, these results suggest that increases in chest redness are mediated by increased blood flow to this area with a concomitant increase in surface temperature. Further research is needed to understand both the energetic costs associated with redness and how other males respond to variation in the signal.

**Keywords** Color · Male competition · Sexual selection · Signal · Skin · *Theropithecus gelada* · Validation

## Introduction

Conspicuous coloration has been favored by natural and sexual selection in a wide variety of both animals and plants. Colorful signals are exhibited in a diversity of contexts, including warning (aposematic) coloration (Lev-Yadun 2001; Exnerová et al. 2003; Siddiqi et al. 2004), mimicry

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(Rettenmeyer 1970), predator confusion (Cuthill et al. 2005), camouflage (Stevens and Merilaita 2011), sexual selection (Keyser and Hill 2000; Houde 2019), and species discrimination (Uy et al. 2009; Kingdon 2010). Among mammals, the primate order tends to be particularly colorful (Caro 2005; Bradley and Mundy 2008), exhibiting a range of pelage and skin colors that has been associated with phylogenetic relatedness (Winters et al. 2020; Bell et al. 2021), individual identity (Parr et al. 2000), sexes (Mourthe et al. 2019), developmental stages (Hendershott et al. 2019), sexual signals (Higham et al. 2013; Rigaill et al. 2019), degrees of UV protection (Jablonski and Chaplin 2010), as well as ambient temperature and humidity (Kamilar and Bradley 2011).

In primates, some of the most conspicuous color variation is associated with sexual signaling. Many primates have colorful sexual skin on their faces (mandrills: Setchell et al. 2006; rhesus macaques: Waitt et al. 2006), genitals (vervet monkeys: Gerald 2001; drills: Marty et al. 2009), and perineal region (chimpanzees: Deschner et al. 2004; baboons: Gesquiere et al. 2007; macaques: Higham et al. 2012; bonobos: Douglas et al. 2016). In female primates, sexual skin coloration can vary with female reproductive status (Dubuc et al. 2009) and fecundity (Dubuc et al. 2014a). In males, colored skin appears to be selected by mechanisms of both inter- and intra-sexual selection, perhaps depending on the relative strength of different mechanisms in different systems. For example, in some species, male color expression has been linked to female mate choice (*Eulemur fulvus* subspecies: Cooper and Hosey 2003; rhesus macaques: Dubuc et al. 2014b), whereas in others it has been linked more commonly to signaling of male social status to other males (geladas: Bergman et al. 2009; vervet monkeys: Gerald 2001; black-and-white snub-nosed monkey: Grueter et al. 2015a; mandrills: Setchell and Dixson 2001).

A particularly striking example of primate coloration is the brilliant red chest patch of male geladas (*Theropithecus gelada,* a species of cercopithecine primate; Fig. 1). The signal may have been under selection for its role in mediating male-male contests. Gelada male contests can be extremely costly (Maynard Smith 1982), and since their large, fluid societies ensure that males often encounter and interact with rival males they do not recognize individually (Bergman 2010), gelada males would benefit from an external signal of strength or condition. In gelada societies, dozens of modular "reproductive units" travel and forage together in "bands". Each reproductive unit comprises a dominant "leader" male and 1–12 adult females and their offspring (Snyder-Mackler et al. 2012a). Approximately one-third of these units also contain one or more subordinate "follower" males that may gain some reproductive opportunities (Snyder-Mackler et al. 2012b). At the periphery of the reproductive units, "bachelor" males form another type of core group (the "all-male group"). Bachelor males lack reproductive opportunities until they overthrow a leader and gain access to that unit's females (or join a unit as a subordinate follower; Pappano and Beehner 2014).

**Fig. 1** Adult male gelada (*Theropithecus gelada*) in the Simien Mountains National Park, Ethiopia. Photo by R. Perlman

Previous research has shown that adult males have redder chests than subadult males (Bergman and Beehner 2008), that leader males have redder chests than bachelor or follower males (Bergman et al. 2009), and that leader males with more adult females in their groups have redder chests than those with fewer females in their groups (Bergman et al. 2009). Specifically, this research proposed that redder chests in leader males may deter takeover attempts from bachelor males. Since males cannot rely on experience from previous encounters to guide each individual rival assessment, gelada males should benefit from a signal that reliably indicates condition and/or fighting ability (Bergman and Sheehan 2013; Grueter et al. 2015b). Indeed, bachelor males are less likely to challenge males with the reddest chests, and leaders with the reddest chests are more likely to maintain their leader status across the subsequent year (Benítez 2016).

We had two primary objectives for this manuscript. Our first goal was to compare multiple methods of color measurement for working with color in wild animal populations. We compared two digital photography color measurement methods: Adobe Photoshop (Adobe Inc. 2021; hereafter "Adobe"), the method used in previous gelada studies (Bergman and Beehner 2008; Bergman et al. 2009) but updated with current software, and the micaToolbox (Empirical Imaging 2021) designed for use with ImageJ (Schneider et al. 2012) which incorporates the visual system of the animal (hereafter "ImageJ micaToolbox"). Specifically, we assessed: (1) whether Adobe and ImageJ micaToolbox methods were consistent across lighting conditions ("Method consistency"), and (2) whether subjective redness scores judged by human observers, Adobe, and ImageJ micaToolbox match values directly measured from the skin in anesthetized animals using a Nix™ Mini Color Sensor (Nix Sensor Ltd. 2021; "Method accuracy").

Our second goal was to examine the physical correlates of chest redness in male geladas. We hypothesized that chest redness in male geladas is linked to blood flow in the skin, similarly to how skin blood flow correlates with sexual skin redness in male rhesus macaques (Rhodes et al. 1997). We examined three variables that should be associated with increased blood flow to the chest patch: high-intensity physical activity, direct heat application, and higher skin surface temperatures. First, we predicted that leader male chest redness would increase after vigorous physical activity that increases blood flow ("Activity and redness"), such as male displays—a ritualized loud-call followed by running, throwing rocks, climbing trees, or shaking branches (hereafter "display"; Benítez et al. 2016). These displays (and their quality and frequency) are thought to deter bachelors who might otherwise challenge leader males (Benítez 2016). Second, we predicted that the application of heat to the skin (Heinonen et al. 2011) would increase chest redness in anesthetized male geladas ("Heat manipulation and redness"). Third, we predicted that leader males with redder chests would have higher surface skin temperature (presumably as a result of increased skin blood flow; "Redness and skin temperature").

# Methods

## Study site and subjects

Field data were collected from wild geladas in the Simien Mountains National Park (SMNP), Ethiopia as part of the Simien Mountains Gelada Research Project (SMGRP). The SMGRP has collected behavioral, demographic, and hormonal data on a population of geladas in the SMNP since 2006, and has conducted annual immobilization campaigns (hereafter, "darting") since 2017. Each year, 20–50 adult male and female geladas are anesthetized with Telinject blowdarts (Telinject USA Inc.) containing ketamine (7.5 mg/kg) and medetomidine (0.04 mg/kg). While the animal is anesthetized, we collect a variety of data, including blood, a skin biopsy, a muscle biopsy, hair, microbiome swabs, chest photos, tooth metrics, and morphological measurements. This is conducted under the supervision of licensed veterinarians and veterinary technicians who monitor the animal's temperature, pulse, and respiration every 10 min. Following data collection, sedation is reversed with atipamezole (0.2 mg/kg). Individuals are monitored during recovery until they return to their social units. During the study period, on average, individuals lifted their heads 18 min after reversal and started walking 42 min after reversal. Every animal successfully returned to their unit by the end of the day. All data were collected with permission from the Ethiopian Wildlife Conservation Authority, and all research was approved by the Institutional Animal Care and Use Committee (for the University of Michigan for non-invasive work: IACUC: PRO00008871; and for the University of Washington IACUC: A120397 and Arizona State University IACUC: 20-1754R for the darting work) and followed all laws and guidelines in Ethiopia. This research conformed to the American Society of Primatologists/International Primatological Society Code of Best Practices for Field Primatology.

## Camera, color standard, and redness metrics

Photographs from the redness and skin temperature dataset were taken with a Nikon COOLPIX 8700, and photographs from all other datasets (method consistency, method accuracy, activity and redness, and heat manipulation and redness) were taken with a Nikon D3200 camera. The camera settings should matter more than the make and model of the camera itself for the implementation of these methods. Although RAW file format is preferred to minimize image processing from the camera and to allow the generation of images that are linear with respect to radiance (Troscianko and Stevens 2015), we collected all photos in JPEG file format. JPEG format was necessary to maintain consistency across datasets, particularly because our long-term database photos were collected in JPEG format. We also note that the primary issue with the use of JPEGs as opposed to RAW images is one of loss of pattern resolution due to lossy compression, which is particularly important when measuring fine pattern details (e.g., the pattern on a butterfly's wing), but which should be less important here (Stevens et al. 2007). To overcome the obstacle of assessing color under variable light conditions, we incorporated the use of a color standard, the X-Rite ColorChecker® Classic chart (hereafter, "ColorChecker chart") to adjust the color in the photograph to the known color levels in the chart squares. The ColorChecker chart is included in the same photo as the gelada ("simultaneous method") for the darting dataset while individuals were anesthetized and in a consecutive photo directly after the photo of the gelada ("sequential method") for all other datasets (Higham 2006; Bergman and Beehner 2008).

Redness metrics differ slightly between Adobe and ImageJ micaToolbox measurements because the two sets of software utilize different color spaces. For Adobe, we used the Adobe RGB (1998) ICC (International Color Consortium) color profile, which uses RGB color space. Similar to previous studies of redness in geladas, we used the Red to Green Ratio (hereafter, "Red/Green") because the value in each RGB channel is only informative relative to values in the other channels (Bergman and Beehner 2008). For ImageJ micaToolbox, we converted measurements to the color space of the *Papio* (baboon) visual system as a proxy for the visual system of *Theropithecus* as the *Theropithecus* visual system has not yet been characterized but spectral sensitivity (the specific light wavelengths to which the cone cells of the retina respond) is highly conserved across cercopithecine monkeys (Jacobs and Deegan 1999). After conversion to the *Papio* visual system, ImageJ micaToolbox measurements were recorded in LW (long wavelength), MW (medium wavelength), and SW (short wavelength) channels. We used Red-Green Opponency (hereafter, "R-G Opponency" (LW − MW)/(LW + MW)) as the redness metric for ImageJ micaToolbox measurements similar to other primate studies (Dubuc et al. 2014a). In our method consistency investigation, we also calculated luminance ((LW + MW)/2), an achromatic measurement of brightness, from ImageJ micaToolbox measurements (Osorio and Vorobyev 2005). We validated luminance along with redness because it has been hypothesized that redness varies with blood oxygenation (redder skin has more oxygenated blood) while luminance varies with skin blood flow (higher blood flow creates darker, less luminous skin), suggesting both may be important metrics for characterizing variation in gelada chest patch color (Changizi et al. 2006; Stephen et al. 2009).

## Data collection

### Method consistency

For the first step of our validation process, we created a validation set of photos following protocols outlined previously for the field (Bergman and Beehner 2008). In brief, the photos of the subject were followed immediately (within 1–2 min) by a second photo of the ColorChecker chart ensuring the ambient light conditions had not changed and that the f-stop and shutter speed of the camera were consistent between the two photos (the sequential method). To simulate this process, we took two photos of the ColorChecker chart: in the first photo, the ColorChecker chart simulated the subject, and in the second photo the ColorChecker chart simulated the color standard. To ensure consistency across lighting conditions, validation photos were taken at various angles and across four light conditions: (1) backlit, (2) cloud, (3) shade, and (4) full sun ($n = 10$ photo sets per condition; 40 photos total).

### Method accuracy

We measured chest patch color on anesthetized geladas using a Nix™ Mini Color Sensor (Nix Sensor Ltd.), a small device that blocks out ambient light, provides its own standardized light source, scans a surface, and records the color in a variety of color spaces (e.g., sRGB, CIELAB). We chose the Nix™ Mini Color Sensor (hereafter, "Nix") because the compact design is useful for field research, and the Nix accurately reproduced published sRGB values when measuring a ColorChecker chart directly (Fig. S1). The Nix measures represent our "gold standard" for color measures because our own Nix values on the ColorChecker chart almost perfectly reproduced the values from the ColorChecker chart itself ($R^2 = 0.99$; Tables S1–S3, Fig. S1). Although the Nix represents our "gold standard" for this validation, it is not useful for routine use because animals must be anesthetized first. The annual SMGRP dartings provided us with opportunities to measure chest color more directly to better assess the accuracy of our methods. We placed the Nix on three different spots on the chest patch and recorded three scans. To directly compare the Nix to the color measurement methods, we took digital photographs of each subject's chest patch and a ColorChecker chart (Bergman and Beehner 2008).

As an alternative metric to the Adobe and ImageJ micaToolbox methods, we assessed the utility of subjective redness scores. Four authors (PMD, RFP, JCB, TJB) independently ranked 44 photos collected from a subset of the darted geladas (11 males and 11 females, $n = 1$–3 photos per ID). Individuals were represented in the dataset in three possible temperature manipulation conditions: (1) baseline, (2) heat pack application, or (3) ice pack application. Each photo was considered a separate data point for subjective redness as authors were blinded to the individual's ID when they viewed the chest photo and scored each photo from 1 (palest) to 5 (reddest). Each photo was given an average subjective redness score compiled from scores across the four observers.

### Activity and redness

To assess the impact of activity level on chest patch redness, we analyzed gelada chest photos collected between 2017 and 2018 from leader males under free-moving conditions (i.e., non-darting photos). In total, we analyzed 13 sets of photos across 7 males, each set comprising one chest photo (and the corresponding ColorChecker chart) taken "post-display" and a complementary "baseline" photo taken within the same month (Sep 2017–Aug 2018). Post-display photos were taken within 10 min of vigorous display activity. Baseline photos were taken when the individual was conducting daily activities like resting, grazing, or grooming at least 10 min after a vigorous display activity. Since previous analyses found that chest redness shows a moderately seasonal pattern (Benítez 2016), we matched each post-display photo to a baseline photo taken within the same month (± 30 days).

### Heat manipulation and redness

We examined whether a heat pack applied to the chest patches of 15 anesthetized male geladas increased chest redness. These data were collected during the 2017–2018 darting season. We took two chest photos within the same frame as the ColorChecker chart (simultaneous method). The first photo was taken at the beginning of the anesthetization. Subsequently, we applied a heat pack on one side of the chest for 1 min and took another photo of that side of the chest with the ColorChecker chart. Each heat pack was activated directly before application, ensuring consistency in the heat condition across study subjects.

### Redness and skin temperature

To assess whether chest redness is associated with chest skin surface temperature, we used a Raytek MX6 PhotoTemp Infrared Thermometer (Fluke Process Instruments; hereafter, "temperature gun") to measure chest skin temperature (˚C) non-invasively from a distance of 1–2 m (Fig. S2). Previous findings indicate daily minimum and maximum ambient temperatures do not impact chest redness (DeLacey et al. 2019). However, to minimize the impact of fluctuations in ambient temperature and seasonality, data were collected in the morning between 8:00 and 11:00 am within a 1-month window. These data were collected in 2007 from 14 adult leader males.

## Photo measurement

### Adobe measurements

Our previous Adobe method utilized a software called inCamera Plugin (PictoColor Software Inc.) which creates a color profile that adjusts the color in the photograph to the known color levels in each square of the chart (Bergman and Beehner 2008; Bergman et al. 2009). However, because the inCamera Plugin is no longer available in the most recent versions of Adobe Photoshop, we validated the Adobe method with new software, ColorChecker Camera Calibration (X-Rite Inc.), that is compatible with Adobe Photoshop 2021. We analyzed JPEG photos in Adobe Photoshop 2021 (22.1.0 release) using color profiles created in ColorChecker Camera Calibration (v2.2.0), software designed for use with the ColorChecker chart.

First, each ColorChecker chart photo was processed in ColorChecker Camera Calibration to create a color profile, which was then used to adjust the color in the accompanying chest photo. We converted JPEG images of the ColorChecker chart to TIFF files to be compatible with the software. Second, we uploaded each TIFF image and aligned the software's 24 square grid with our ColorChecker chart image. Third, we selected "Create Profile" to create an ICC color profile. These profiles automatically save to a folder that is accessible to Adobe Photoshop. Color standard photos where there was "clipping", when the light levels (0–255) for the RGB channels reach the upper limits of the camera (255), were discarded (Stevens et al. 2007).

After creating the profiles, we measured the photographs in Adobe Photoshop following previous protocols established for geladas (Bergman and Beehner 2008). We assigned and converted the color profile specific to that photo. Following color correction, we used the "rectangular marquee" tool to select an area of the chest (minimum 500 pixels) and recorded the mean of the Red, Green, and Blue channels of the selected area using the "histogram" tool (Fig. S3). Since skin color is not uniform across the chest patch, we developed protocols for selecting areas of the chest to maintain consistency across measurements. We selected the flattest area possible on the lateral corner of the chest patch while avoiding areas of dirt or dry, flaking skin. We also avoided measuring medial areas of the chest because the chest rounds inward creating a convex surface with inconsistent lighting.

### ImageJ micaToolbox measurements

The micaToolbox (Empirical Imaging 2021), designed for use with ImageJ (Schneider et al. 2012), offers a free and open-source software suite to calibrate non-linear digital images and convert images to the visual system (i.e., cone-catch values) of a wide variety of animals to measure color, luminance, and pattern information (Troscianko and Stevens 2015). The micaToolbox was initially designed for use with RAW file formats only. A recent update, however, allows the use of JPEG images (i.e., non-linear images) which expands its utility for long-term field sites such as ours that may only have stored JPEG images for analysis (van den Berg et al. 2020). JPEG photos were analyzed in ImageJ (v1.52a) with the micaToolbox (v2.0.2) (Schneider et al. 2012; Troscianko and Stevens 2015).

To accurately quantify color in a JPEG image, an extra transformation step is necessary to linearize the image (van den Berg et al. 2020). To create a linearization model in ImageJ, we used a high-quality JPEG image of the ColorChecker chart. Using the micaToolbox, we specified six gray standard reflectance values (squares 19–24), which creates numerous model linearization curves for the camera using a range of different equations. We selected the best fitting model based on the highest coefficient of determination ($R^2$) between the measured pixel values and the standard reflectance values of the six gray standards of the ColorChecker chart (in this case, the JT Linearisation model). We applied the selected model to all JPEG images, and for each image we generated a "multispectral image", a stack of images taken at different ranges of wavelengths, specifying the "white" square (91.57% standard reflectance) and "black" square (3.22% standard reflectance) as the gray standards for each image. The gray standards can be selected either in the same photo or in a different photo, allowing for use of either the simultaneous or sequential method.

Next, we converted the image using a cone-catch model, which corrects for both the camera's spectral sensitivity (i.e., the camera's relative efficiency to detect light) and the visual system of the study animal. We used micaToolbox to characterize the Nikon D3200 camera sensitivity using a photo of the ColorChecker chart which we then applied to all images (van den Berg et al. 2020). *Papio* cone-catch sensitivities were calculated using a rhodopsin template, developed by Govardovskii et al. (2000) and adapted for use in primates (Osorio and Vorobyev 2008), based on peak spectral sensitivities of Guinea baboons (*Papio papio*) ($\lambda_{max} = 565.5$, 536.5, 428; Bowmaker et al. 1991).

Lastly, we used the rectangle tool in ImageJ to select the chest patch as the region of interest (ROI) and measured the mean and standard deviation of each channel in the ROI. The polygon selections tool in ImageJ can be used to select a larger region (e.g., the entire chest patch), but to ensure direct comparison between methods, we selected the same rectangular area of the chest to measure in both the Adobe and ImageJ methods. We then recorded the long wavelength (LW), medium wavelength (MW), and short wavelength (SW) values (Fig. S4).

## Data analyses

All statistical analyses were performed in R version 4.0.2 (R Core Team 2020).

Linear models were run in the R package lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). Inter-rater reliability was assessed in the R package irr (Gamer et al. 2019). Plots were constructed with R packages ggplot2 (Wickham 2016) and ggpubr (Kassambara 2020).

### Method consistency

Following Bergman and Beehner (2008), we measured the "light skin" and "moderate red" squares in each set of photos (these square names are not our own, but assigned by the ColorChecker chart and maintained in this publication for easy reference), which span the range of color observed in gelada male chest patches. For each of the two squares, we ran linear regression models, with redness as the outcome variable and light condition (cloud, backlit, shade, sun) as the predictor variable to quantify variation in measurements between light conditions. Redness was quantified as Red/Green for the Adobe method and R-G Opponency for the ImageJ micaToolbox method. We also ran two separate linear regression models with luminance as the outcome variable and light condition as the predictor variable for the "light skin" and "moderate red" squares for the ImageJ micaToolbox method. One cloud condition data point was discarded from all datasets because the f-stop and shutter speed differed between the paired set of photos.

### Method accuracy

To compare measurements with the Nix "gold standard", we ran three separate linear regression models with the Nix values as our independent variable to the (1) subjective redness scores, (2) redness measured with Adobe, and (3) redness measured with ImageJ micaToolbox to determine which metric was nearest to the values obtained from the Nix. All independent variables were standardized with a z-score before running linear regression models to enable comparison across different redness metrics. Inter-rater reliability was assessed using a two-way mixed, consistency, average-measured intra-class correlation (hereafter, "ICC") (McGraw & Wong 1996; Hallgren 2012) with an ICC of 0.75–1.0 (Cicchetti 1994) required to confirm a high degree of agreement in redness ratings.

### Activity and redness

To assess whether redness increased after post-display activity for leader males, we ran a paired *t*-test of redness between baseline and post-display activity levels measured with Adobe. We assessed normality with Quantile–Quantile plots and a Shapiro–Wilk normality test for baseline and post-display redness. A Shapiro–Wilk test revealed that both "baseline" ($W(13) = 0.92$, $p = 0.248$) and "post-display" ($W(13) = 0.898$, $p = 0.124$) redness variables are normally distributed, and we proceeded with a parametric paired t-test.

### Heat manipulation and redness

To examine whether our experimental application of a heat pack to the chest increased male chest redness, we ran a paired t-test of redness between photos from the same male taken at baseline and after heat application. We assessed normality with Quantile–Quantile plots and a Shapiro–Wilk normality test for baseline and heat manipulation redness. A Shapiro–Wilk test revealed that both baseline ($W(15) = 0.95$, $p = 0.528$) and heat application ($W(15) = 0.89$, $p = 0.068$) redness variables are normally distributed, and we proceeded with a parametric paired t-test. One individual was excluded from analyses as an outlier because the baseline redness value was over 1.5*IQR above the mean and over 2 SD above the mean.

### Redness and skin temperature

To identify whether leader males with redder chest patches have higher skin surface temperatures, we ran a linear regression model of chest temperature (outcome variable) as a function of chest redness.

## Results

### Method consistency

For Adobe Photoshop, the sole difference in measurements across light conditions was the "light skin" square measured in the backlit condition ($b=0.052$, $\mathrm{SE}=0.005$, $t=7.620$, $p<0.001$; Fig. 2A; Table S4). Note that this difference is of small magnitude (the difference in means across light conditions is only 6.5% of the difference between the two color patches).

For ImageJ micaToolbox, there were several significant differences across light conditions; in particular, the "light skin" square measured in the backlit condition ($b=-0.008$, $\mathrm{SE}=0.001$, $t=-5.767$, $p<0.001$) and the "moderate red" square measured in the shade ($b=-0.009$, $\mathrm{SE}=0.004$, $t=-2.285$, $p=0.030$) and sun conditions ($b=-0.010$, $\mathrm{SE}=0.004$, $t=-2.487$, $p=0.019$; Fig. 2B; Table S5). Some differences were significant but also of small magnitude (the largest difference in means across light conditions is only 10.9% of the difference between the two squares). Luminance measured with ImageJ micaToolbox did not vary by light condition for either the "light skin" or "moderate red" square ($p>0.05$; Fig. 2C; Table S6).

### Method accuracy

Redness measures from all three methods were highly correlated with the Nix scores with the closest association between the subjective redness scores ($F(1,42)=103.7$, $R^2=0.71$, $p<0.001$, Fig. 3A), followed by the Adobe chest redness values ($F(1,42)=36.75$, $R^2=0.47$, $p<0.001$, Fig. 3B), followed by the ImageJ micaToolbox chest redness values ($F(1,42)=20.73$, $R^2=0.33$, $p<0.001$, Fig. 3C). Note that although statistics are calculated with z-scores, we plot the raw values in our figures below. Our method validation suggests that Adobe Photoshop (or subjective scores) are best suited for chest redness scores under field conditions. For all remaining results, the figures represent Adobe results (for figures employing ImageJ micaToolbox, see supplemental Figs. S5–7). Inter-rater reliability assessment confirmed that authors had a high degree of agreement in subjective redness ratings, $\mathrm{ICC}=0.942$.

### Activity and redness

For the paired baseline and post-display chest patch values, recent displays by males ("post-display") produced redder chest patches for the same males when compared to their own "baseline" photos (paired $t$-test: $t=2.58$, $df=12$, $p=0.024$, Fig. 4; ImageJ results did not demonstrate redder ($p=0.26$) or lower luminance ($p=0.97$) chest patches for males immediately after a display, Fig. S5).

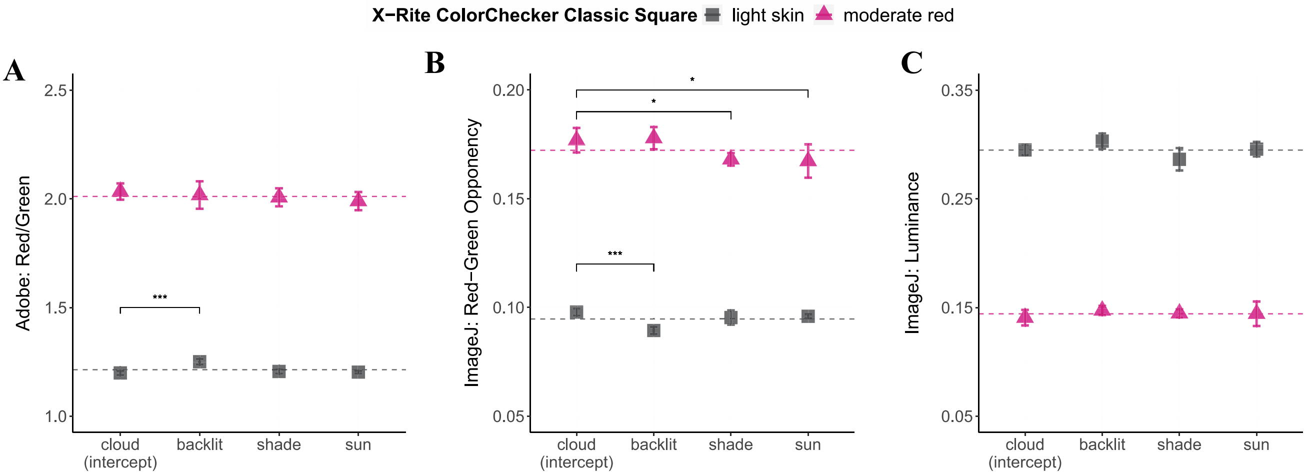

**Fig. 2** Method consistency: Adobe and ImageJ micaToolbox across four lighting conditions for two colored squares on the X-Rite ColorChecker chart. Variation across lighting conditions for the "light skin" and the "moderate red" colored squares for: **A** Red/Green measured in Adobe. **B** R-G Opponency ((LW − MW)/(LW + MW)) measured in ImageJ micaToolbox. **C** Luminance ((LW + MW)/2) measured in ImageJ micaToolbox. Dotted lines represent the average values for each square for photos across all light conditions. Error bars represent the standard error of the mean

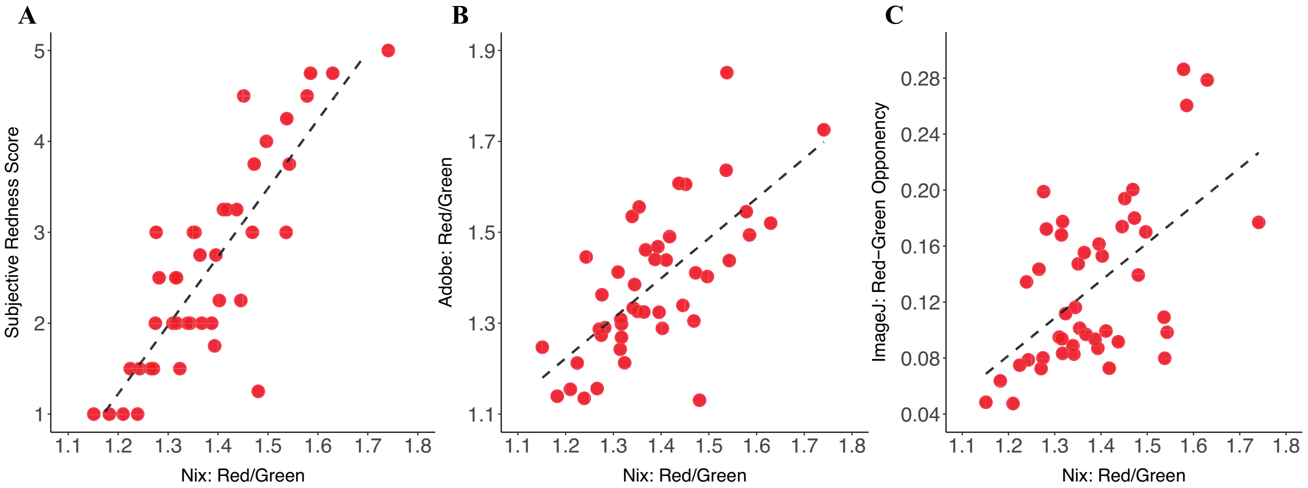

**Fig. 3** Method accuracy: redness measures from all three methods were significantly correlated with the Nix measurement. The relationship between the Nix chest redness values (Red/Green) and **A** subjective redness scores averaged across all observers, **B** Adobe Photoshop chest redness values (Red/Green), and **C)** ImageJ micaToolbox chest redness values (Red-Green Opponency (LW − MW)/(LW + MW))

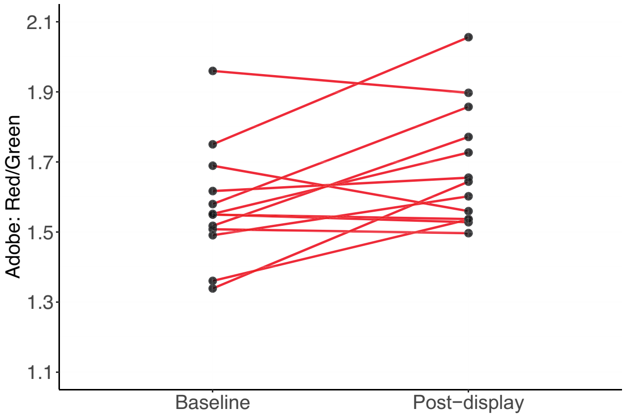

**Fig. 4** Activity and redness: male chests were redder immediately after a display ("post-display") compared to "baseline"

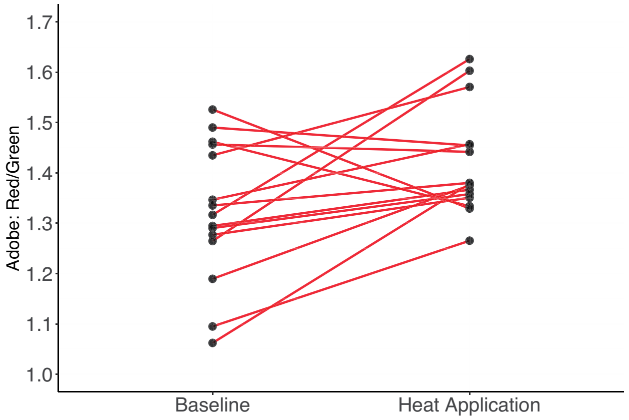

**Fig. 5** Heat manipulation and redness: male chests were redder immediately after a heat application compared to before ("baseline")

### Heat manipulation and redness

Within individuals, chest redness (Red/Green measured in Adobe) increased after direct application of a heat pack to the chest for 1 min compared to baseline conditions (paired t-test: $t = 2.41$, $df = 14$, $p = 0.03$, Fig. 5; ImageJ results also found that chest redness increased after direct application of a heat pack to the chest ($p = 0.02$), but chest luminance did not change between baseline and heat application ($p = 0.8$), Fig. S6).

### Redness and skin temperature

Chest skin surface temperature increased with chest redness (Red/Green) in adult males as measured with Adobe Photoshop ($b = 4.016$, SE = 1.526, $t = 2.632$, $p = 0.022$), Fig. 6; ImageJ results also indicated that chest skin surface temperature increased with chest redness ($p = 0.03$) and trended towards decreasing with luminance ($p = 0.09$), Fig. S7).

## Discussion

We validated two methods, Adobe and ImageJ micaToolbox, across four lighting conditions (Fig. 2) and in comparison to Nix redness measurements taken directly on the chest of immobilized geladas (Fig. 3). We used the Adobe method to show that increased chest redness is associated with increased activity, local application of a heat pack, and higher skin surface temperature (Figs. 4, 5 and 6). Together, these results suggest that one of the main sources of an increase in chest redness in gelada males derives from

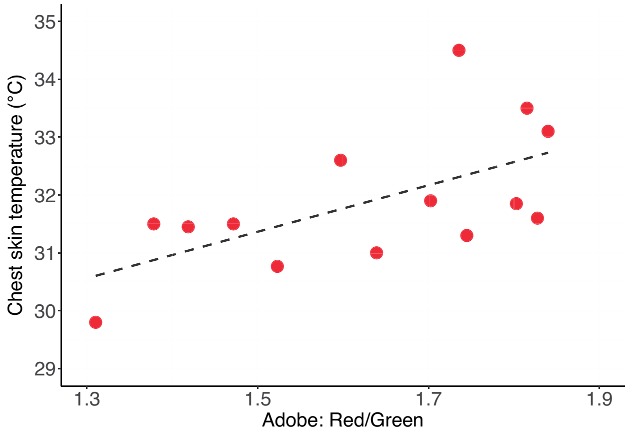

**Fig. 6** Redness and skin temperature: redder chests have higher skin surface temperatures. Chest patch surface temperature (℃) measured with a Raytek MX6 PhotoTemp Infrared Thermometer increases with chest redness (Red/Green) in leader males

increased blood flow with a concomitant increase in surface temperature. This finding elucidates for the first time a mechanism by which color variation is produced and maintained in geladas, and also a mechanism that can link variation in the signal to variation in individual condition.

The complexities of a sexually selected system increase the importance of minimizing measurement errors. One of our goals was to help researchers choose appropriate methods for working with color in the wild. Our results suggest that the Adobe method performed slightly better in terms of consistency across light conditions and in comparison to the Nix direct skin measurements. Both Adobe and ImageJ micaToolbox methods were fairly consistent across a wide range of light conditions and correlated with the Nix redness measurements. Although redness measurements for backlit light conditions varied from other light sources for both methods, the differences were small (Fig. 2). Among the metrics compared to Nix, ImageJ micaToolbox had the weakest correlation (Fig. 3). This could be attributed to the ImageJ micaToolbox method only using two gray standards from each paired ColorChecker chart rather than all 24 squares (including the "light skin" square and "moderate red" square that are close in color to the chest patch) as the Adobe method does. In addition, our use of JPEG images could have contributed to the relatively poor performance of ImageJ micaToolbox as the software was only recently adapted for use with JPEGs and functions best with RAW file formats (van den Berg et al. 2020). Finally, it is possible that, by correcting for the visual system of the subject, the ImageJ micaToolbox results are capturing something that is biologically relevant to the geladas but is not apparent to us (or detected by the other methods that were developed for the human visual system).

In our study, the subjective classifications had the strongest correlation with Nix measures compared to objective color measures. This result suggests that older methods of color classification in primates that use the human eye remain entirely relevant for primate color analyses (particularly for catarrhine primates). However, humans will naturally have differences in color perceptions, and this trend could be subject to low experimental repeatability if adopted in long-term research with many different observers (Endler 1990). In addition, although human subjective measures may be useful for studying the visual perception of a catarrhine primate with a similar visual system to humans (Bowmaker et al. 1991; Jacobs and Deegan 1999), visual systems vary widely across animals and include those with the ability to see spectra not visible to humans (e.g., UV). In studies on animals that have spectral sensitivities with less overlap with humans, ImageJ micaToolbox would be the preferred method as it allows conversion of images to the cone-catch sensitivity of the animal and has capabilities for UV-sensitive cameras (Troscianko and Stevens 2015; van den Berg et al. 2020). In addition, the ImageJ micaToolbox offers a suite of tools for studying contrast and pattern which the Adobe method does not provide (van den Berg et al. 2020). In studies on wild populations where the animal is immobilized, the Nix measurement method may be the most useful, as is a lightweight tool for measuring color that has been proven effective for measuring pelage, feathers, or skin in museum specimens (Potash et al. 2020). However, Nix measurements are designed for human visual systems which limits its use to animals with similar visual systems to humans.

We found that chest redness increased with activity ($p < 0.05$), heat application ($p < 0.05$), and skin surface temperature ($p < 0.05$), and chest luminance tended to decrease with skin surface temperature ($p = 0.09$, Fig. S7B), although the difference was not statistically significant, all supporting the more general hypothesis that chest redness in gelada males is associated with increased blood flow. The activity associated with male displays temporarily increased a male's chest redness (Fig. 4). Displays in geladas (and the activity and vocalizations that accompany them) are hypothesized to be used by leader males to ward off challenging bachelors—similar to chacma baboons (*Papio ursinus*), where adult males give a contest call with acoustic properties tied to rank that mediates male-male aggression by preventing fights between disparately ranked males (Kitchen et al. 2003). The change in chest color for post-display male geladas likely results from increased blood flow to the area due to elevated heart rate and blood pressure resulting from the increase in activity. In humans, exercise increases skin blood flow to dissipate heat generated by contracting muscles (Johnson 1986; Kenney and Johnson 1992), and in rhesus macaques, high skin blood flow increases skin redness (Rhodes et al.

1997). This suggests that redness in geladas might relate to overall activity levels and might explain some of the differences found across leader males. However, we do not know whether these brief episodes of activity might also increase longer term *baseline* redness for these males. We would like to know how long these transient increases in redness persist and whether differences in basal metabolic activity are associated with differences in baseline redness. In addition, the variation in redness among leader males could also reflect the oxygen content of their blood because red skin coloration can be produced by increased oxygenation (Changizi et al. 2006). In a high-altitude environment like the Simien Mountains National Park where the oxygen is only about 66% that at sea level (Tinsley Johnson et al. 2018), this could be a salient factor limiting male fighting ability.

We also found that experimentally increasing the temperature of the chest on immobilized males temporarily increased chest redness (Fig. 5). We suggest that this trend is caused by the local effects of vasodilation, which has been shown to increase skeletal muscle blood flow in humans (Heinonen et al. 2011). This suggests that some of the differences in redness across males are due to differences in the local control of blood flow to the chest patch. Permanent developmental changes in this regulation could explain the observation of increases in redness in males that transition from bachelor to leader (Bergman et al. 2009). We propose that one-time ontogenetic regulatory changes associated with becoming a leader male result in a local, sustained increase in blood flow to the chest patch. This suggests that only males who have gone through this developmental switch regulate blood flow to their chest differently than other geladas. This potential developmental switch resembles signals triggered by social circumstances in other primates like the Bornean orangutan (*Pongo pygmaeus*), where cheek-pads (flanges) develop only for dominant males (Kuze et al. 2005), and mandrills (*Mandrillus sphinx*), where dominant males with access to mating opportunities exhibit a larger morphological variant (fatted; Wickings and Dixson 1992).

Finally, we found that redder chests have a higher surface temperature (Fig. 6). This is likely a result of increased blood flow to the skin, and may be a signal production cost for the maintenance of redder chest patches. The ability of males to withstand a higher rate of heat loss may indicate a greater metabolic capacity, which is particularly salient for a species that regularly experiences below-freezing temperatures (Tinsley Johnson et al. 2018). In addition, the lower partial pressure of atmospheric oxygen may amplify the level of cold that animals experience in high-altitude environments (Hayes 1989; Chappell and Hammond 2004; Milledge et al. 2007; Cheviron et al. 2013). In golden snub-nosed monkeys (*Rhinopithecus roxella*), for example, a decrease of 5–10 degrees in winter months is associated with an energetic deficit, which suggests even small annual fluctuations in temperature can have a sizable impact on primate metabolic demands (Hou et al. 2020). To reduce heat loss, cold-adapted homeotherms often decrease energy expenditure by altering their behavior (Terrien et al. 2011). In geladas, we routinely see males and females sit with heads lowered over their chest patches on cold mornings, resulting in less exposed chest patches; they also huddle together with chest patches facing inward, which may also serve to reduce heat loss (Fig. S8). Huddling behavior for thermoregulation has been observed in other primates that live in extreme environments (titi monkeys, *Callicebus nigrifrons*: Gestich et al. 2014; ring-tailed lemurs, *Lemur catta*: Kelley et al. 2016); golden snub-nosed monkeys, *Rhinopithecus roxellana*: Hou et al. 2020) and has been demonstrated to effectively conserve energy expenditure (vervet monkeys, *Chlorocebus pygerythrus*: McFarland et al. 2015) and increase body temperature (Japanese macaques, *Macaca fuscata*: Hanya et al. 2007). Although we found that redder chests are associated with higher surface temperatures, we cannot yet determine whether this heat loss incurs a meaningful metabolic cost. Future research using non-invasive metabolic indices will help to determine how energy balance relates to chest redness.

Together, these findings move us closer to understanding the potential information content of red chests. Our findings suggest that redder chests can indicate males with sufficient energetic reserves to either maintain high rates of physical activity or to offset the metabolic costs of losing heat by directing blood flow specifically to the chest patch (or both). This information is particularly relevant to bachelor males because takeover challenges can be physically demanding battles of attrition that can last for days (Pappano and Beehner 2014). Therefore, attending to chest redness may allow bachelor males to avoid challenging the males who are most likely to win such a contest. However, further research is needed to better understand both the energetic costs associated with redness and how other males respond to variation in redness.

It might seem extravagant that geladas—found only in a high-altitude, cold environment—are the only primate with a bare patch of highly vascularized skin on their chest. Signals are, however, not wasteful over-investments (Penn and Számadó 2019). They evolve because selection favors efficient and optimal investment into signal expression, and some individuals can afford to invest much more in this expression and some much less. Individuals are expected to allocate their investment into their own signal according to their own ability and condition. For example, moths invest less in an anti-predatory signal (that happens to impair thermoregulation) in cold environments (Lindstedt et al. 2009). Particularly in extreme environments, animals that are doing well despite the harsh conditions will be the most able to invest in a signal that flouts the specific risks posed by the extreme environment. Thus, it is probably not a coincidence that geladas, living at both a temperature and oxygen extreme, appear to have a sexual signal associated with vasodilation, heat loss, and possibly even oxygen saturation. Gelada leader males that communicate their ability to overcome these constraints and bachelor males that attend to this information will both have an advantage. Therefore, signal form might match a species' environment not only in terms of efficacy of transmission (Patricelli and Hebets 2016) but also in the type of information it can potentially convey. For geladas, the mix of red-colored blood signaling and an extreme cold environment may have provided an elegant demonstration of the natural links between signal form and function.

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**Author contributions** Conceptualization, data curation, formal analysis, investigation, visualization: PMD, RFP, JCB, TJB; data collection: PMD, RFP, SS, ISC, KLC, AL, FA, NSM, JCB, TJB; writing—original draft: PMD, RFP, JCB, TJB; writing—review and editing: all the authors; supervision: JCB, TJB. All the authors reviewed the results and approved the final version of the manuscript.

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## Declarations

**Conflict of interest** On behalf of all the authors, the corresponding author states that there is no conflict of interest.

**Data availability** Data and code are available at https://github.com/GeladaResearchProject/DeLacey_Perlman_et_al_chest_color_2022.

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