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Is Brightest Best? Testing the Hamilton-Zuk Hypothesis in Mandrills

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Abstract Although many primates exhibit striking coloration, including brightly colored pelage and bare areas of skin, our understanding of the function and evolution of these traits pales in the face of knowledge about color in other taxa. However, recent years have seen an increase in the number of studies of individual variation in primate color and evidence is accumulating that these traits can act as important signals to conspecifics. Mandrills are arguably the most colorful of all primates. Here, we review what we have discovered about the signal function of coloration in male and female mandrills from our long-term studies of a semi-free-ranging colony in Franceville, Gabon and test the predictions of the Hamilton-Zuk hypothesis—that bright coloration is condition dependent, and that only individuals of superior quality will be able to express color fully—in this species. We compare measures of facial coloration in both sexes with parasite load (using fecal analysis over 1 annual cycle), immune status (hematological parameters), neutral genetic

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diversity (microsatellite heterozygosity), and major histocompatability (MHC) genotype to examine whether red coloration acts as an honest signal of individual quality in mandrills. We found that red coloration was unrelated to parasitism and hematological parameters. Red was also unrelated to genome-wide heterozygosity and MHC diversity, although specific MHC genotypes were significantly related to red. The healthy, provisioned nature of the colony and problems associated with observational, correlational studies restrict interpretation of our data, and it would be premature to draw conclusions as to whether color signals individual quality in mandrills. We conclude with some suggestions for future studies on the signal content of color in mandrills and other primates.

Keywords handicap · heterozygosity · immunocompetence handicap hypothesis · lymphocytes · MHC · parasite-mediated sexual selection · parasites · secondary sexual traits

Introduction

Female mating preferences have led to the evolution of extreme male ornamentation throughout the animal kingdom (Andersson 1994; Darwin 1871). However, the reasons underlying female preference for ornamented males remain a matter of debate (Andersson 1994; Kokko *et al.* 2003), particularly in non-resource-based mating systems where females receive only genes from males (Kirkpatrick and Ryan 1991). Handicap theories of mate choice propose that exaggerated secondary sexual ornaments, such as bright coloration, are condition dependent, and that only individuals of superior quality will be able to express costly ornamentation (Zahavi 1975). In particular, the Hamilton-Zuk hypothesis suggests that secondary sexual ornaments may reliably reflect ability to resist parasites by revealing current health status (Hamilton and Zuk 1982; Moller and Saino 1994). An extension of this, the immunocompetence handicap hypothesis, holds that testosterone-dependent ornaments signal the ability to cope with the immunosuppressive effects of testosterone (Folstad and Karter 1992). Members of the opposite sex will choose the most ornamented mate because these mates provide fitness benefits, either directly, through avoidance of parasite transmission and increased investment in offspring or both, or indirectly, as "good genes" for vigor and health that will be passed on to offspring (Able 1996; Andersson 1994; Hamilton and Zuk 1982; Zahavi 1975). Conspicuous traits that serve as honest indicators of viability may also function as status signals in intrasexual competition (Berglund *et al.* 1996).

According to these hypotheses, exaggerated ornaments may signal a high level of genetic heterozygosity, either across the entire genome (Brown 1997) or at particular coding loci. High levels of genome-wide heterozygosity are associated with increased survival and fitness (Keller and Waller 2002), probably because genetic diversity reduces the likelihood that recessive deleterious alleles will be expressed (Charlesworth and Charlesworth 1987) and increases the number of potentially useful gene products (Edwards and Hedrick 1998; Jennions and Petrie 2000; Mitton *et al.* 1993; Penn and Potts 1999; von Schantz *et al.* 1996). If more heterozygous animals possess increased metabolic efficiency (Mitton *et al.* 1993), disease

resistance (Acevedo-Whitehouse *et al.* 2003; Aparicio *et al.* 2001), or both, then this may allow them to afford the cost of producing secondary sexual traits better than homozygous animals (Brown 1997). Heterozygous animals would therefore be more attractive as mates and more intimidating to rivals. Individuals are unable to pass on heterozygosity at specific loci and the indirect (genetic) benefits of mate choice for traits indicating a high degree of heterozygosity are unclear (Brown 1997; Mays and Hill 2004; Partridge 1983). Heterozygous individuals are therefore thought to confer direct, rather than indirect, fitness benefits to their offspring (Mays and Hill 2004; Partridge 1983).

If ornaments signal diversity at particular coding loci, then one of the best candidates is the major histocompatibility complex (MHC; Jordan and Bruford 1998; Penn and Potts 1999). The MHC is a multigene family encoding cell-surface glycoproteins that play a critical role in immune response by recognizing foreign peptides, presenting them to specialist immune cells and initiating an appropriate immune response (Klein 1986). MHC loci are highly polymorphic and diversity is selectively maintained, at least in part, via pathogen-mediated selection (Apanius *et al.* 1997). Increased MHC heterozygosity may enhance an individual's ability to resist pathogens, by increasing the repertoire of immune responses (Penn and Potts 1999). This, in turn, would allow individuals to invest in costly displays. Certain MHC genotypes may also be advantageous if they provide resistance to common parasites. Links between individual MHC genotypes and particular parasites have been demonstrated in various species (Bernatchez and Landry 2003), supporting this possibility.

There is now evidence that exaggerated ornament expression in males is related to parasitic infection or immune status in many animal species (Andersson 1994; Johnstone 1995; Møller *et al.* 1999; Zuk 1992). Likewise, secondary sexual traits have been shown to correlate positively with genetic diversity, or to decrease with inbreeding, in male birds (Aparicio *et al.* 2001; Foerster *et al.* 2003; von Schantz *et al.* 1996, 1997) and fish (Müller and Ward 1995; Sheridan and Pomiankowski 1997; van Oosterhout *et al.* 2003). However, to our knowledge, the relationship between heterozygosity and secondary sexual traits has been investigated in only 1 species of mammal, the white-tailed deer (*Odocoileus virginianus*), where antler growth in males correlates positively correlated with heterozygosity at multiple protein-coding loci (Scribner *et al.* 1989) and with MHC diversity (Ditchkoff *et al.* 2001). Moreover, studies of secondary sexual ornaments and their maintenance by sexual selection have tended to focus on males (Andersson 1994), although females may also possess showy ornaments (Amundsen 2000). Female ornaments have been assumed to represent a by-product, or "correlated response," of selection for ornamentation in males (Darwin 1871; Lande 1980). However, a review of studies in birds concluded that there was strong evidence that female ornamentation is not severely constrained by selection on males, and that female ornaments, like those of males, are maintained via contest competition and mate choice (Amundsen 2000).

Colorful Primates

Many primates, of both sexes, exhibit brightly colored areas of skin: usually red or blue sexual skin on the perineum, genitalia, and adjacent areas (Bradley and Mundy,

2008; Dixson 1998; Gerald 2003). While a great deal of work has been carried out on the signal function of bright coloration in other species (Andersson 1994; Hill 2006), until recently, little work has focused on primate color. The difficulties of studying sexual selection in primates are well known (Setchell and Kappeler 2003). However, in the case of color, primatologists have an advantage over researchers studying species with signals that are undetectable to the naked human eye: Old World monkeys have very similar trichromatic color vision to humans (Jacobs and Deegan 1999; Yokoyama and Yokoyama 1989). Recently, interest in the possible signal function of primate color has grown markedly, as highlighted by this special issue of the *International Journal of Primatology*. Experiments have demonstrated that differences in blue scrotal coloration can predict the outcome of interactions between pairs of unfamiliar males in male vervets (*Cercopithecus aethiops*; Gerald 2001). Female rhesus macaques (*Macaca mulatta*) gaze longer at images of red male faces than they do at pale images of the same males (Waitt *et al.* 2003), and the authors interpret these results in the context of mate choice, suggesting that females prefer to mate with redder males. Red coloration in male mandrills acts as a badge of status (Setchell and Wickings 2005) and attracts females (Setchell 2005). In humans, wearing red leads to an increased chance of success in closely matched sport competitions (Hill and Barton 2005), and men find images of women more attractive when they are viewed against a red background, or wear a red shirt, although they are unaware that color influences their ratings (Elliot and Niesta 2008).

Reports concerning various primate species suggest a relationship between coloration and condition or health status. Specifically, the red skin coloration of the bald uakari (*Cacajao calvus*) fades when they are parasitized (Ayres 1996; Lasry and Sheridan 1965), blue scrotal coloration in vervets fades during periods of poor nutrition (Isbell 1995), and coat color in female brown lemurs (*Eulemur fulvus*) is negatively related to parasite load (Regan 1998). These findings strongly suggest that coloration may act as an honest signal of quality to prospective mates, potential rivals, or both. Only 1 study has yet investigated the relationship among color, parasites, hematological parameters, and genetic quality in primates in detail, finding no support for the hypothesis that female sexual swelling reliably signals female health or genetic diversity (Setchell *et al.* 2006a).

Mandrills

Mandrills (*Mandrillus sphinx*) are arguably the most colorful primates. Both males and females show red and blue coloration on the face and anogenital region, with dramatic interindividual variation in expression (Setchell *et al.* 2006d; Wickings and Dixson 1992b). Mandrills occur only in the dense rain forest of central Africa (Grubb 1973) and have proved extremely difficult to study, and impossible to habituate, in the wild (Abernethy *et al.* 2002; Harrison 1988). Studies at Lope National Park (Gabon) provide a tantalizing glimpse into mandrill socioecology and suggest that mandrills travel in large, semi-disaggregated bands in which males and females may not have direct knowledge of male quality (Abernethy *et al.* 2002; Harrison 1988). Indicators, such as color, may therefore be more important for this species than for related species, such as macaques or baboons, in which males and females have more stable, longer-term relationships (Setchell and Kappeler 2003).

We have been fortunate to study a semi-free-ranging colony of mandrills at the Centre International de Recherches Médicales de Franceville, Gabon (CIRMF). While there are obvious problems associated with studying a semi-free-ranging colony, including the influence of provisioning, and a lack of gene flow (Setchell *et al.* 2005b), the colony represents a useful approximation of natural conditions. In addition, it provides the unique possibility of long-term study of known individuals and captures for collection of morphological data, blood, and other biological samples. Studies of the CIRMF colony suggest that mandrill groups are made up of stable female matrilines (Setchell 1999). Male ranks are less stable, but there is always 1 α-male, while other males vary in the extent to which they associate with the social group (Setchell and Dixson 2001a; Wickings and Dixson 1992b). Male-male competition for access to receptive females is intense, and the α-male in the colony is responsible for 77-100% of mate-guarding in any one breeding season and sires 33-100% of the offspring born in any one birth season (Setchell *et al.* 2005a). Mating is costly for males, in terms of time and energy invested and the risk of aggression both from other males (Setchell and Wickings 2006) and from females (Setchell *et al.* 2005c), and males also show mate choice by preferentially allocating mating effort to higher quality females (Setchell and Wickings 2006).

Red coloration begins to develop at the age of 6 yr in male mandrills, along with a suite of other secondary sexual characteristics, and increases until the age of *ca.* 10 yr, when males also reach full adult body size (Setchell and Dixson 2002; Setchell *et al.* 2006c). Individual variation in male red, but not blue, color is linked to age, dominance status and testosterone levels (Setchell and Dixson 2001a, b, 2002; Setchell *et al.* 2008; Wickings and Dixson 1992a, b). The α-male is usually the reddest male in the group (Setchell and Dixson 2001a), although this is not always the case because red coloration develops once a male has attained top rank, and newly α-males take time to develop their full color (Setchell *et al.* 2008). Similarly, loss of rank leads to decreased red color (Setchell and Dixson 2001b). Thus, red represents an honest signal of current androgen status, competitive ability and willingness to engage in fights with other males (Setchell *et al.* 2008). Males use the relative brightness of their red coloration to facilitate the assessment of individual differences in fighting ability (Setchell and Wickings 2005). In addition to the role it plays in male-male competition, red is also involved in mate choice as females prefer to mate with redder males, independent of their attraction to dominant males (Setchell 2005).

In contrast to male redness, facial red in female mandrills is unrelated to rank or measures of reproductive success (age at first birth or mean interbirth interval; (Setchell *et al.* 2006d). This sex difference is likely to be due to the different reproductive priorities of the 2 sexes and to differences in their modes of competition (Trivers 1972). However, facial color does increase significantly with age in females, and primiparous females are darker than multiparous females. Color is also brighter during the follicular phase than during the luteal phase of the menstrual cycle. It varies across gestation and peaks at 4 and 8 wk postparturition (Setchell *et al.* 2006d). Females also have pink-red sexual swellings, the brightness of which is also unrelated to female rank and measures of reproductive success (Setchell and Wickings 2004). However, in contrast to facial color, swelling brightness decreases with increasing age and with increasing body condition, but is unrelated to female rank or parity (Setchell and Wickings 2004).

Here we examine the relationship among facial red color and parasite levels, hematological parameters, and genetic diversity in male and female mandrills, to evaluate whether ornamentation provides an honest signal of quality in this species. If red color reliably indicates fitness in terms of parasite resistance (Hamilton and Zuk 1982), then individuals with low parasitism should be more colorful than those with high parasitism. Similarly, if red color indicates immune system quality (Moller and Saino 1994), and the ability to withstand the immunosuppressive effect of high testosterone levels (Folstad and Karter 1992), then individuals with better than average general immune status (hematological parameters) should be more colorful than those with lower than average general immune status. If red indicates genome-wide heterozygosity (Brown 1997) or MHC genotype, then individuals with greater genome-wide heterozygosity, more diverse MHC genotypes, or both, should be more colorful than those with lower heterozygosity and MHC diversity. Finally, if red coloration advertises possession of specific "good genes," then we predict a relationship between specific MHC genotypes and red coloration. Due to sex differences in reproductive competition, and our previous findings concerning sex differences in the correlates of red color, which suggest that female red is not sexually selected (Setchell *et al.* 2006d) and may approximate the ancestral state (Cotton *et al.* 2004), we predict that these relationships are more likely to be true for males than for females.

Methods

Study Population

The CIRMF mandrill colony was established in 1983/4, when 15 individuals (7 males, 8 females) originating from the wild, were released into a 6.5-ha naturally rain-forested enclosure (Enclosure 1). All further additions to the group have been due to reproduction of the founder individuals, while some individuals have been removed. CIRMF established a second semi-free-ranging group in 1994 (in Enclosure 2, 3.5 ha) by transferring 17 mandrills (including 4 adult males and 6 adult females) from the first enclosure. The monkeys forage freely in the enclosure, and receive daily supplements of monkey chow and seasonal fruits. Water is available *ad libitum*.

CIRMF records the date of birth for all individuals born into the colony, and we approximated the age of founder individuals from their previous history and dental records. We recorded female reproductive status, births, dominance ranks, injuries, and disappearances daily during 1996–2005. Primate Centre staff captured all monkeys for a routine veterinary control at least once annually, when we were able to obtain blood samples for blood cell counts and genetic analyses.

Group sizes during the study ranged from 31 to 86, with 9–26 reproductive females and 2–10 adult males (Setchell *et al.* 2006c), corresponding to smaller groups occurring in the wild (Hoshino *et al.* 1984; Rogers *et al.* 1996). Male subjects were all 44 males that attained the age of 6 yr in the colony (the age at which males begin to develop secondary sexual traits; Setchell and Dixson 2002) and for whom photographs and capture data were available (no data were available for 2 males).

Female subjects included all 43 females aged≥3 yr present in the colony during 2003–2005 (age 3.5–26.6 yr, mean 9.7 yr). Coloration and microsatellite genetic data were available for all subjects. MHC, parasite, and hematological parameter data were available for various subsets of males and females.

Quantifying Color

We measured facial red using scanned photographic records (1989–2003, males only) and digital images captured via a Nikon Coolpix 5700 digital camera and saved as fine quality jpeg files (2003–2005, males and females). All images used were of monkeys when they were in either an open grassy area or in an open feeding pen. Images required calibration to account for light drift (Gerald *et al.* 2001). It was impossible to obtain images of subjects in the same frame as a photographic black-and-white standard or to place a standard in the same position as the subject and capture a second image immediately after that of the subject. Therefore, we used only images in which color ranged the full spectrum from white to black and used the Autolevels command in Adobe Photoshop 6.0 (Image Mode set to RGB) to define the lightest and darkest pixels in each color channel as white and black. This method may result in the loss of some variation in color due to saturation (where images appear to contain fully white colors but where the true color seen went beyond that measurable at the exposure used; Stevens *et al*., this issue).

Once calibrated, we outlined the entire midnasal strip in a standard fashion using the polygonal lasso tool in Adobe Photoshop 6.0. We measured the mean luminosity and the mean red intensity value (mean number of pixels at each intensity level) of the highlighted area using the Image > histogram command. We found that the gray score from the red channel, divided by luminosity, produced color measures that correlated best with quantified color chart assessments of the same colors (Setchell and Dixson 2001a; Setchell *et al.* 2006c, d). Although we are aware that this method introduces scatter or "noise" to the data set, there is no reason to believe that it introduces systematic bias. Further, we have found a range of significant results in mandrills using these methods (Setchell *et al.*, 2006c, d, 2008), showing that it is possible to find significant results in predicted directions using them, and that the "noise" induced by our methods is not likely to be the cause of an absence of significant results in the present study. Where available, we used the mean value for multiple images of the same individual for each age class (N=1–13 images, mean± SEM 9.3±4.3).

Quantifying Parasitism

We estimated parasitic infection using fecal parasite analysis (Setchell *et al.* 2007). We collected 1–3 fecal samples per month for all males aged >7 yr and all parous females in E1 between April 2004 and March 2005 (N=874 fecal samples). We collected samples immediately after defecation during morning (1000 h–1130 h) or afternoon (1530 h–1730 h) observation periods. We homogenized the feces and stored a portion (mean ± SEM: 7.6±0.1 g) in 20 ml of 10% formalin solution for analysis by an independent parasitologist who had no knowledge of the individuals concerned. He examined samples using direct smears and centrifugation/flotation

using a Sheather's solution at a specific gravity of 1.18. He recorded parasitic eggs, larvae, trophs, and cysts by species according to characteristic morphology and quantified these as 0 (none), 1 (1–5), 2 (6–10), and 3 (>10).

We quantified general levels of parasitism for only the 20 males and 14 females for whom samples were available for ≥6 of the 12 mo, to avoid any systematic bias, as:

1) Abundance: Mean abundance of cysts or eggs of each taxon in the feces (scale of 0–3 above)
2) Prevalence: Mean monthly presence of each taxon (number of samples in which a particular taxon occurred divided by the number of samples, expressed as a percentage)
3) Richness: Mean monthly species richness (number of taxa found in the feces)

We have described general patterns of parasite prevalence, abundance, and diversity in the mandrill colony elsewhere (Setchell *et al.* 2007). Briefly, we found 3 taxa of amoebic protozoa (*Entamoeba coli*, *Endolimax nana*, and *Entamoeba histolytica/dispar* complex), 1 ciliate protozoa (*Balantidium coli*), and various nematodes in fecal samples collected from focal individuals during the study period. The abundance and prevalence of *Entamoeba coli* and *Enodolimax nana* and the prevalence of *Balantidium coli* did not show sufficient interindividual variation to be informative in comparisons with red coloration, because they were present in all (*Entamoeba coli* and *Enodolimax nana*) or almost all samples (Setchell *et al.* 2007).

Quantifying Immune Status

The Laboratoire des Analyses Médicales at CIRMF conducted all hematological analyses using blood samples taken via venipuncture during captures. We have described the hematological parameters of the mandrills in detail elsewhere (Setchell *et al.* 2006b). We measured general immune status using absolute counts of lymphocytes, which are involved in adaptive recognition of antigens, phagocytes (neutrophils and monocytes), which fight off pathogens, and eosinophils, which play a role in killing helminth parasites (Meeusen and Balic 2000; Roitt *et al.* 1998). Using relative counts (proportion of all white blood cells) did not alter the significance of our results. We also calculated the ratio of neutrophils to lymphocytes. An increase in this ratio indicates a reduction in immune function, and is related to stress in primates (Kim *et al.* 2005). Blood cell counts were available for 28 males and 31 females.

Quantifying Neutral Genetic Diversity

We genotyped all 219 focal subjects for 6–8 microsatellite loci (mean ± SEM: 7.89±0.05) using blood samples collected during annual veterinary captures. We estimated genetic diversity using internal relatedness (IR), which weights each genotype by the frequencies of the alleles involved, such that rare allele homozygotes are given more weight than homozygotes for common alleles (Amos *et al.* 2001).

The more an individual is genetically diverse, the more IR is negative. We have previously shown that our measure of IR is a good measure of genome-wide inbreeding in this population (Charpentier *et al.* 2005).

Quantifying MHC Diversity

We conducted MHC-DRB genotyping for a large subset (155) of the mandrill population (insufficient DNA was available for the remaining individuals). Mandrill MHC class II genes are highly polymorphic (Abbott *et al.* 2006) and mandrill MHC-DRB sequences are under strong positive selection pressure with the peptide binding region (PBR) containing significantly more nonsynonymous than synonymous changes (Abbott *et al.* 2006), suggesting that this area of the genome is under balancing selection. We PCR amplified MHC-DRB sequences and analyzed products using denaturing gradient gel electrophoresis (DGGE) followed by direct sequencing as described in Abbott *et al.* (2006). We amplified DNA samples from each individual multiple times and repeated all genotyping experiments to ensure that any sequence found in 1 individual would also be detected in all other individuals in the population. We excluded all –DRB6 sequences from the statistical analyses reported here, as these are typically a nonfunctional pseudogene in other primates (Klein and O'hUigin 1995). However, including these sequences in analyses did not alter the significance of results.

We used MHC sequence data to define supertypes. Supertypes are groups of MHC-DRB alleles that share peptide-binding motifs and are therefore functionally similar (Doytchinova and Flower 2005), and have been shown to be biologically relevant in studies of both human and nonhuman primates (Schwensow *et al.* 2007b; Southwood *et al.* 1998; Trachtenberg *et al.* 2003). We determined supertypes by identifying variable amino acid positions, presumed to represent the peptide binding region, using phylogenetic analysis of MHC sequences in MEGA 4 (Tamura *et al.* 2007). We then used PAML 4 (Yang 2007) to identify positively selected sites (PSS). Finally, we identified supertypes by analyzing the chemical specificities of these PSS in Genesis version 1.7.2 (Sturn *et al.* 2002), following Doytchinova and Flower (2005) and Schwensow *et al.* (2007b).

We measured the MHC diversity of each individual in 3 ways:

1) The number of different MHC alleles possessed. The MHC-DRB region in Old World primates is characterized by frequent gene duplication and deletion, respectively (Slierendregt *et al.* 1994). As a consequence, individuals not only vary in the alleles found at any locus but also in the number and variety of genes found on a haplotype. We therefore focused on the number of different sequences possessed by an individual as a measure of MHC diversity, without making any assumptions about the number of loci involved (Aeschlimann *et al.* 2003; Ekblom *et al.* 2004, 2008; Málaga-Trillo *et al.* 1998).

2) MHC allele diversity. We calculated allele diversity as the mean number of amino acid differences between all MHC alleles possess by an individual (Landry *et al.* 2001). This may be more informative than the number of sequences possessed, because MHC alleles may differ in nucleotide composition, but be functionally similar in terms of immune defense if the protein they encode binds the same peptides (Rammensee 1995; Sidney *et al.* 1995).

3) The number of different MHC supertypes possessed. Again, this may be more informative than the number of sequences possessed as supertypes group sequences that share peptide-binding motifs, and are therefore functionally similar (Doytchinova and Flower 2005).

Statistical Analyses

Individuals contributed multiple data points for red coloration (males: 1–43, mean 13.5, females: 4–42, mean 26.0), rank (males: 1–6, mean 2.8, female rank is stable over time), and hematological parameters (males: 1–6, mean 2.9, females: 1–2, mean 1.7) during the study. Because age is known to influence these variables (Setchell *et al.* 2006b, c, d), we calculated standardized residuals for age using locally weighted least-squares regressions for each sex (proc LOESS: SAS version 9; f=0.4, 10 iterations). This method is useful in that it produces an estimated average value for each age without assuming any underlying form for the curve (Moses *et al.* 1992). We calculated "residuals" for each data point as the natural logarithm of the ratio of the observed value to the expected value (Moses *et al.* 1992). We refer to these residuals as red-for-age, rank-for-age (males only) and counts-for-age for the various hematological parameters. In males we term red-for-age values "male-red." In females, reproductive status (gestating, lactating, or cycling) is also known to influence facial red color significantly (Setchell *et al.* 2006d), so we used a general linear model (SAS version 9, GLM procedure for normally distributed residuals) fitting reproductive status to the red-for-age values to obtain residuals that represent red-for-age-for-status. We term these values "female-red." Collectively, we term male-red and female-red "red."

We investigated the relationship between red and other variables using general linear models (SAS version 9, GLM procedure), because residuals were always normally distributed. "Red," parasite data and hematological parameters were all available for different time periods during the study. To investigate the relationship between red and each parasite measure we considered only the period for which both parasite and red data were available, and compared the mean value of red (mean-red) for each individual during that period with the mean parasite measures for that individual. To investigate the relationship between red and hematological parameters we used hematological parameters that matched the period for which we had data for red, i.e., 1996–2005 for males, 2003–2005 for females, and compared mean-red for each individual during that period with the mean hematological parameters for that individual. Finally, we investigated whether genotype (IR and the various measures of MHC genotype) predicted red using mean-red calculated using all data available for red, because the genotype is constant for a given individual. We weighted all analyses by the number of data points that each individual contributed for red to avoid any bias due to under-represented individuals. We included rank-for-age (males) or absolute rank (females) as a covariate in all models. Sample sizes varied with analysis, due to our combining various data sets, and are reported with the statistical results.

We also conducted analyses using general linear mixed models, including individual ID as a random effect in models to incorporate multiple observations of

the same individuals. Results were qualitatively the same, and we report only results of the GLM procedures.

Results

We found no relationship between mean-red and parasite measures (Table I) or hematological parameters (Table II) in either males or females. We also found no relationship between mean-red and IR in either males (N=44, $F_{1,42}$=0.20, p=0.66) or females (N=43, $F_{1,41}$=0.34, p=0.56).

We found no significant relationships among mean-red and the number of MHC alleles possessed, amino acid diversity, or the number of supertypes possessed by an individual mandrill (Table III). However, we did find significant relationships between mean-red and the possession of individual MHC supertypes: S4 and S11 were positively associated with mean-red in males, while S3 and S8 were both negatively associated with mean-red in females (Table III).

Discussion

We found no significant relationships between red color and individual quality, measured as parasitism and immune status (hematological parameters), or between red color and genetic diversity (MHC diversity or genome-wide heterozygosity), in the CIRMF mandrills. Our results do not support the Hamilton-Zuk hypothesis, which predicts that individuals with low parasitism and high-quality immune systems should show more exaggerated ornaments than those with high parasitism and poorer immune systems (Hamilton and Zuk 1982; Moller and Saino 1994). Nor do our results support the "good genes as heterozygosity" hypothesis (Brown 1997), which holds that exaggerated ornaments signal a high level of average heterozygosity. This suggests that we may need to turn to alternative hypotheses to explain why mandrills are so extraordinarily colored, such as the sexy son hypothesis (Fisher 1930). However,

Table I Relationships between mean-red and parasitism

	Balantidium coli abundance	*Entamoeba histolytica/dispar* complex abundance	*Entamoeba histolytica/dispar* complex prevalence	Nematode abundance	Nematode prevalence	Species richness
Males (N=20)	$F_{1,18}$=0.02, p=0.89	$F_{1,18}$=1.17, p=0.30	$F_{1,18}$=0.81, p=0.38	$F_{1,18}$=0.02, p=0.89	$F_{1,18}$=0.01, p=0.93	$F_{1,18}$=0.03, p=0.87
Females (N=14)	$F_{1,12}$=0.07, p=0.79	$F_{1,12}$=0.32, p=0.58	$F_{1,12}$=0.36, p=0.56	$F_{1,12}$=1.67, p=0.22	$F_{1,12}$=0.34, p=0.63	$F_{1,12}$=0.11, p=0.74

Parasite estimates are means for each individual

One GLM analysis was performed for each parasite estimate.

Entamoeba histolytica and *Entamoeba dispar* are identical under the microscope and are therefore reported as *Entamoeba histolytica/dispar* complex (Setchell *et al.* 2007).

Table II Relationships between mean-red and hematological parameters

	Lymphocytes	Neutrophils	Monocytes	Eosinophils	Ratio neutrophils /lymphocytes
Males (N=28)	$F_{1,26}$=3.32, p=0.08	$F_{1,26}$=1.23, p=0.28	$F_{1,26}$=0.80, p=0.38	$F_{1,26}$=0.74, p=0.40	$F_{1,26}$=0.03, p=0.86
Females (N=31)	$F_{1,29}$=0.11, p=0.75	$F_{1,29}$=0.00, p=0.97	$F_{1,29}$=0.05, p=0.83	$F_{1,29}$=3.56, p=0.07	$F_{1,29}$=0.41, p=0.52

Hematological parameters are mean counts-for-age for each individual

One GLM analysis was performed for each hematological parameter.

several caveats suggest that it would be premature to conclude that red color in mandrills is not a reliable indicator of individual quality.

First, although the CIRMF mandrill colony allows us to investigate important questions about a fascinating and unusual primate in the best situation in which it can be studied, one should use caution when generalizing from this closed population to wild mandrills (Setchell *et al.* 2005b). For example, we found surprisingly little interindividual variation in parasitism (Setchell *et al.* 2007), by comparison with natural primate populations (Nunn and Altizer 2006; Stuart and Strier 1995). Some of the parasite taxa we identified in the mandrills are known to be pathogenic (Setchell *et al.* 2007), and mediating the effects of infection is likely to be physiologically costly. However, the presence of intestinal parasites is well tolerated in the colony (Setchell *et al.* 2007), and our investigation of relatively healthy individuals limits the usefulness of this test. Study site constraints on color methods both reduce variation in, and add scatter to, our data set, due to our inability

Table III Relationships between mean-red and MHC genotype

	Males (N=40)	Females (N=36)
Number of MHC sequences possessed	$F_{1,38}$=0.01, p=0.92	$F_{1,34}$=0.69, p=0.20
Amino acid sequence diversity	$F_{1,38}$=2.39, p=0.13	$F_{1,34}$=0.06, p=0.80
Number of supertypes possessed	$F_{1,38}$=0.14, p=0.71	$F_{1,34}$=0.09, p=0.77
S1	$F_{1,38}$=0.01, p=0.94	$F_{1,34}$=1.32, p=0.26
S2	$F_{1,38}$=0.33, p=0.57	$F_{1,34}$=2.77, p=0.11
S3	$F_{1,38}$=0.82, p=0.37	$F_{1,34}$=5.34, p=0.031*
S4	$F_{1,38}$=6.19, p=0.020*	$F_{1,34}$=0.90, p=0.35
S5	$F_{1,38}$=0.05, p=0.83	$F_{1,34}$=3.32, p=0.08
S6	$F_{1,38}$=0.46, p=0.50	$F_{1,34}$=3.64, p=0.07
S7	$F_{1,38}$=1.18, p=0.29	$F_{1,34}$=0.63, p=0.44
S8	$F_{1,38}$=0.17, p=0.68	$F_{1,34}$=11.47, p=0.003*
S9	$F_{1,38}$=0.64, p=0.43	$F_{1,34}$=1.41, p=0.25
S10	$F_{1,38}$=0, p=0.98	$F_{1,34}$=2.44, p=0.13
S11	$F_{1,38}$=4.48, p=0.044*	$F_{1,34}$=1.14, p=0.30

One GLM analysis was performed including all variables.

*Indicates results significant at p<0.05.

to include color standards in images or to use the sequential method (Stevens *et al.*, this issue) for standardizing for light. Nonetheless, our methods have detected a range of significant results in predicted directions in mandrills previously (Setchell *et al.* 2006c, d, 2008), suggesting that these problems are not the source of an absence of significant results here.

Second, costly sexual advertising is a life-history trait that trades off with other components of reproduction and survival (Gustafsson *et al.* 1995; Hoglund and Sheldon 1998; Kokko *et al.* 2002). It is, therefore, difficult to draw conclusions from correlative tests of relationships between condition and secondary sexual traits. Indeed, it is possible to use both positive and negative relationships as support for the Hamilton-Zuk hypothesis (Kokko *et al.* 2002; Norris and Evans 2000). This issue should not apply to our test of the relationship between red color and heterozygosity. However, even poor quality mandrills may receive sufficient resources in this provisioned colony to produce bright color, confounding any relationships between color and individual genetic quality.

Third, white blood cell counts may be confounded by the immune response to current infections (Norris and Evans, 2000). Although our use of multiple points for each individual should ameliorate this, provisioning is likely to reduce the variance in measures of condition in comparison with the wild. Thus a stronger relationship between coloration and condition may occur under natural conditions.

Finally, we did detect some interesting relationships between particular MHC supertypes and red coloration, which warrant further investigation. For example, particular MHC alleles are associated with pathogen susceptibility in female fat-tailed dwarf lemurs (*Cheirogaleus medius*; Schwensow *et al.* 2007a). We are currently investigating how individual supertypes influence measures of health and fitness in the mandrill colony.

So Why Are Mandrills Red?

If red color does not provide a reliable signal of individual health or genetic quality, why should female mandrills show preference for red males (Setchell 2005), and males base their interactions on relative color (Setchell and Wickings 2005)? Red in male mandrills is a dynamic trait that mirrors changes in male physiology relatively rapidly, providing an up-to-date signal of competitive ability (Setchell and Dixson 2001b; Setchell *et al.* 2008). Bright, and extensive, red coloration therefore signals that a male is adult, in his prime, and of high status (Setchell *et al.* 2006c, 2008). Moreover, the extent of red color on the face and body increases with time spent as α-male (Setchell *unpub. obs.*), meaning that red may advertise not only high status but also the length of time for which a male has been able to maintain that high status. Such variables may be more related to demography, in terms of the other males that happen to be available (Setchell *et al.* 2006c), than to individual traits such as health or genetic quality, such that any influence of quality on red is diluted by other variables. Males may avoid redder males due to advertised high testosterone and thus willingness to fight.

Female mandrills may choose red males because these are usually the highest ranking males available, and will provide direct benefits in terms of offspring protection. Infanticide is thought to have been a strong selective force in the

evolution of primate reproductive strategies (van Schaik 2000) and is known to occur in mandrills (Setchell *et al.* 2006c). Although male mandrills exhibit little parental care, sire-offspring dyads show more affiliation than dyads consisting of a male and an unrelated infant (Charpentier *et al.* 2007), and possible sires protect infants and juveniles aggressively during annual captures (Setchell *unpub. obs*.). Studies of baboons, a closely related species also characterized by a multimale, multifemale mating system, have shown that the presence of the sire enhances offspring fitness (Charpentier *et al.* 2008), suggesting that paternal influences on offspring success may be more prevalent than previously supposed.

Finally, bright coloration on the face, rump, and genitalia is just one of a suite of secondary sexual characters that occur in male mandrills, which also possess a sternal scent-marking gland, a yellow beard, a long mane of hair, an epigastric fringe, and a "fatted" rump (Hill 1970; Setchell *et al.* 2006c; Wickings and Dixson 1992b). Why do such exaggerated ornaments occur in this particular species? One possible explanation is linked to the fact that mandrills live in dense rain forest, and in very large groups, including many males that appear to move and out of the group (Abernethy *et al.* 2002). Under such situations, conspecifics may not have access to reliable, up-to-date behavioral information on which to base their interactions. "Badges of status," such as testosterone-dependent color, may allow males to assess the competitive ability and willingness to fight of unfamiliar opponents, and to avoid battles that are likely to be costly to both participants (Rohwer and Ewald 1981; Setchell and Wickings 2005). Similarly, females faced with potential mates that are unfamiliar, or are not encountered sufficiently often to give the females up-to-date information on male status, may rely on ornaments to identify suitable mates. The fact that similar traits also occur in other primate species that form very large groups, e.g., drills (*Mandrillus leucophaeus*: Marty *et al.*, this issue) and geladas (*Theropithecus gelada*: Bergman *et al.*, this issue), or where adult males are widely dispersed, e.g., orangutans (*Pongo* spp.) supports this hypothesis (Setchell and Kappeler 2003).

Future Directions

Studies of wild mandrills are clearly needed to resolve the question of whether red coloration signals health and genetic quality. However, it is difficult to envisage how these could be conducted, and it may be more practical to turn to a species that is easier to study in the wild. In addition, future studies of ornamentation in primates should examine the relationship between red coloration and levels of other hormones. Red color in mandrills and other primate species is known to be related to testosterone (Dixson 1998; Setchell *et al.* 2008). However, testosterone is only one of several hormones that may influence the expression of secondary sexual characters (Folstad and Karter 1992; Hillgarth and Wingfield 1977). For example, subordinate individuals may suffer elevated glucocorticoid levels due to stress (von Holst 1998; Wasser and Barash 1983), which suppresses the immune system (Sapolsky 2002), and may prevent them from producing color.

While we have a relatively good understanding of the function of male color in mandrills, we still know little concerning the meaning of female color. Different reproductive priorities in the 2 sexes (Trivers 1972) mean that it is unlikely that color

signals the same information in males and females. We have previously shown that female color changes across the menstrual cycle in mandrills (Setchell *et al.* 2006d), suggesting that it may indicate (or conceal) the fertile phase, as suggested for sexual swellings (Nunn 1999). Future studies should examine the relationship between color and the menstrual cycle in more detail (Dubuc *et al*., this issue; Higham *et al.* 2008), and investigate the hormonal basis of female color.

Experiments using digitally altered images (Waitt *et al.* 2003), or artificial color treatments (Gerald 2001) also have the potential to further our understanding of whether male and female mandrills attend to differences in color between and within individuals of both sexes. For example, a series of experiments have shown that female rhesus macaques attend to differences in male facial color; males attend to the color of female hindquarters, but not faces; while females attend to differences in female faces and hindquarters, suggesting that the signal function of red skin and the intended recipients vary from one anatomical region to another (Gerald *et al.* 2006; Waitt *et al.* 2003, 2006).

Finally, future work should use experimental techniques to examine the relationships among pathogen load, response to immune challenge. and ornamentation (Cotton *et al.* 2004; Norris and Evans 2000). For example, studies could measure color before and after administering antiparasite medication.

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