



Darwin's Roadmap to the Curriculum: Evolutionary Studies in Higher Education

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Charles Darwin and Selection in Relation to Sex in the Colors of Monkeys

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Abstract and Keywords

This chapter explores how Darwin's theory of sexual selection has structured research on primate coloration. Darwin was fascinated by the conspicuous colors displayed by many animals and pointed to primates as a particularly colorful and interesting group. The chapter provides an overview of Darwin's theory of sexual selection, highlighting how different selective mechanisms can lead to the extravagant colors found in many primate species. The chapter then overviews both modern and historical studies of primate coloration, emphasizing how methodological advances and a resurgence of interest in sexual selection has led to a modern revival of Darwin's ideas regarding primate coloration. Finally, the chapter concludes with a discussion of future questions and possible directions of this research. Darwin's collected works clearly show that he was captivated by the bright colors displayed by many primates, and his theory of sexual selection remains the key to understanding the evolution of many of these impressive traits.

Keywords: Darwinism, evolution, evolutionary studies, primate coloration, sexual selection, Charles Darwin, evolutionary biology

MANY ANIMALS EXHIBIT STRIKING colors and patterns that have long fascinated naturalists and stimulated them to ask the question: Why are animals often so colorful? Darwin provided a roadmap for understanding how we might investigate these questions through the lens of natural and sexual selection. Thanks to Darwin, Wallace, and other pioneering evolutionary biologists, we now approach this question by asking: How and why might such conspicuous colors have evolved? In some cases, conspicuous coloration evolves via natural selection, such as warning colors that advertise the toxicity or unpalatability of an animal to potential predators (i.e., aposematic colors; Poulton 1890; Ruxton, Sherratt, & Speed, 2004). Many conspicuous colors, however, appear to have evolved via sexual selection, facilitating an individual's access to a greater number or higher quality of mates. Darwin was fascinated by questions regarding animal coloration; his collected works include many descriptions of animals exhibiting brilliantly colored ornaments, and he used many examples of animal color patterns to support his theories. Darwin's conceptualization of sexual selection, relayed primarily in his 1871 book *The Descent of Man*, was in part an attempt to understand and explain how animals evolved these types of conspicuous ornamentation.

In his paper "Sexual Selection in Relation to Monkeys," published in the journal *Nature* in 1876, Darwin wrote, "No case interested and perplexed me so much as the brightly-coloured hinder ends and adjoining parts of certain monkeys" (p. 18; Figure 6.1). It is no wonder that Darwin (**p.98**) emphasized the brilliant colors of primates. Comfortably the most colorful group of mammals, primates exhibit extensive variation in color and patterning across species (Bradley & Mundy, 2008; Caro, 2005). This is precisely the type of variation that captivates biologists, from early evolutionists like Darwin to modern practitioners using his theories to understand animal diversity. Like other animals, the colors displayed by primates are influenced by both natural and sexual selection as primates seek to both avoid predators and obtain mates. Among primates, natural selection tends to produce cryptic colors that render them difficult to spot against the background, whereas conspicuous primate colors tend to be selected through reproductive contexts and result from sexual selection (Bradley & Mundy, 2008). In this chapter, we explore how Darwin's theory of sexual selection has influenced and structured research focusing on the evolution of conspicuous coloration in primates (Figure 6.1).

Sexual Selection: Darwin's Roadmap to Understanding the Extravagant Colors of Monkeys

Darwin presented the theory of sexual selection in *The Origin of Species* (1859) and greatly expanded it in *The Descent of Man and Selection in* (p.99)

Relation to Sex (1871) to explain the evolution of elaborate traits that are often differentiated by sex and appear to hinder survival. Sexual selection, he wrote in *The Origin of Species*, "depends, not on a struggle for existence . . . but on a struggle between the individuals of one sex . . . for the possession of the other sex. The result is not death to the unsuccessful competitor but few or no offspring" (p. 88). Traits evolve under sexual selection because they increase an individual's lifetime

reproductive success through a competitive advantage in reproduction. Darwin believed this competition took two distinct forms: intrasexual selection, which selects for traits that assist in competition among individuals of the same sex for reproductive opportunities with the opposite sex, and intersexual selection, which selects for traits that improve an individual's attractiveness to the opposite sex. While sexual selection acts on both sexes, albeit to different degrees depending on which sex is the limiting resource to reproduction (Bateman, 1948; Gowaty, 2004; Trivers, 1972), intrasexual and intersexual selection are commonly referred to as male-male competition and female mate choice, respectively.



Figure 6.1. Images of male mandrills. According to Darwin (1871, p. 292), "no other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill". (Color figure in online version.)

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Intrasexual selection often leads to the evolution of armaments to assist in competition (e.g., the horns, tusks, and canines of many mammals), either directly in fights or indirectly by advertising competitive ability (Darwin, 1871). In comparison, intersexual selection leads to the evolution of ornaments that are attractive to potential mates (Clutton-Brock & McAuliffe, 2009; Darwin, 1871) such as the elaborate plumage of many birds (Hill & McGraw, 2006). Due to the tendency of mammalian females to group together to avoid predation in terrestrial habitats where they can be corralled and monopolized by males, mammals are often subject to high degrees of direct male-male contest competition. This results in a high degree of sexual dimorphism in body size, in addition to the evolution of weaponry in males. Primates have evolved classic intrasexually selected traits such as sexual dimorphism in body and canine size, but unusually among mammals, primate males also exhibit brightly colored visual signals (Figure 6.2). Similarly, unlike other mammals, females of many primate species also exhibit colorful ornamentation.



History of Primate Coloration Research

Scientists and philosophers have long been interested in animal coloration, with texts on this topic tracing back to ancient times (e.g., Aristotle, 400 BCE/1910). With the development of his theory of sexual selection in **(p.100)** the 19th century, Darwin (1871) gave biologists a framework by which to investigate how and why mating traits have evolved. The modern study of the evolution of conspicuous animal coloration in mating contexts, including in primates, has its roots in Darwinian thinking.

Figure 6.2. Primates exhibit a wide variety of conspicuous colors that may have evolved under sexual selection. Composite image from Allen and Higham (2013). Top row: bald uakari *Cacajao calvus* (Olpaat), ring-tailed lemur *Lemur catta* (Yves Picq), emperor tamarin *Saguinus imperator* (B. Inaglory), mantled guereza *Colobus guereza* (C. Burnett). Middle row: mandril *Mandrillus sphinx* (R. Young), De Brazza's monkey *Cercopithecus neglectus* (W. Allen), Diana monkey *Cercopithecus neglectus* (W. Allen). Bottom row: common squirrel monkey *Saimiri sciureus* (T. Montfort), crowned guenon *Cercopithecus pogonias* (W. Allen), gelada *Theropithecus gelada* (Kolumbusjogger), collared mangabey *Cercocebus torquatus* (W. Allen). (Color figure in online version.)

In providing support for his new theory of sexual selection, Darwin drew examples from a wide variety of taxa, including primates. He generally considered conspicuous primate colors to have evolved in males via female mate choice. These conclusions were based on observations of primate morphology (e.g., color patch location and color change across time) and behavior (e.g., the presentation of colorful regions during socio-sexual interactions; Darwin, 1876). Although Darwin brought attention (**p.101**) to primate colors as important examples of sexual selection, it would be over a century before much research was conducted in this area. Early Darwinists and their opponents used animal coloration extensively as support for their views on the process of evolution (Blaisdell, 1992); however, this work focused primarily on natural selection. The theory of sexual selection was less well received than that of natural selection, with many early evolutionists expressing doubts about its validity (e.g., Wallace 1870, 1889) and seeking alternative explanations. In an extreme example, Thayer (1909) considered all animal colors to have evolved under natural selection for crypsis; even the peacock's tail, now a textbook example of a sexually selected trait, was considered by Thayer to have evolved for concealment in flowering trees. Research on coloration in nonhuman primates was also rare during this time, with the majority of this work focused on other taxa such as birds and insects. Information about primate colors is notably absent from Poulton's volume *The Colours of Animals*, published in 1890, as well as Cott's impressive tome *Adaptive Coloration in Animals*, published half a century later in 1940. Both of these books were heralded by contemporaries as impressive and comprehensive works, and the lack of references to primates within their pages is representative of the general lack of research at the time.

Historically, the majority of research on conspicuous coloration and sexual selection in primates that did occur was focused on the sexual skin of Old World monkeys and apes. Primate sexual skin is a region of largely hairless skin, often in the hindquarters, genitals, and/or face, that can vary in color across time (Dixson 1983, 2012). Females of some species also exhibit varying degrees of swelling of perineal sexual skin, called sexual swellings (Zinner, van Schaik, Nunn, & Kappeler, 2004).

Many studies analyzing the coloration of primate females' sexual skin were published throughout the 20th century. Much of the earlier work in this area was physiological in nature, focusing primarily on how changes in sexual skin color are tied to hormones and the reproductive cycle. These studies did not generally emphasize an evolutionary perspective or attempt to understand the signaling function of sexual skin based on sexual selection, but they did provide useful information for later researchers. For instance, researchers demonstrated that sexual skin color changes are linked to female reproductive cycling (Baulu, 1976; Corner, 1932; Czaja, Eisele, & Goy, 1975; Elder & Yerkes, 1936; Gillman & Gilbert, 1946; Heape, 1896; Matthews, 1956; Zuckerman, van Wagenen, & Gardiner, 1938), pregnancy status (Altmann, 1973; Baulu, 1976; Bielert et al., 1976; Gilbert & Gillman, 1945, 1951; Hartman, 1928; Tinklepaugh & Hartman, **(p.102)** 1930), and breeding seasonality (Baulu, 1976; Koford, 1965). They also showed that sexual skin color changes across development (Zuckerman et al., 1938), that red sexual skin is caused by increased vascularization of the relevant tissue (Collings, 1926), that color saturation is linked to estrogen and progesterone levels (Corner, 1935; Czaja, Robinson, Eisele, Scheffler, & Roy, 1977), and that hormone receptors mediating these changes are found in the sexual skin (Kato, Onouchi, & Oshima, 1980; Onouchi & Kato, 1983; Ozasa & Gould, 1982). Some early investigators, however, did explicitly tie their research back to Darwin and sexual selection theory. For instance, Pocock (1906) concluded that conspicuous female sexual skin may "reveal to the males the sex and condition of adult non-pregnant females . . . act[ing] as an aphrodisiac impelling them to pair with the females in which the characters are produced rather than with those in which they are poorly developed or absent" (p. 560).

Darwin's sexual selection framework emphasized colorful ornamentations used to obtain mates by males, however, and the use of similar ornamentations by females was originally not well understood. Explicit links between female sexual skin and sexual selection were initially rare but became more common later in the 20th century as these ideas became more developed. For instance, a number of hypotheses were put forth to explain how colorful sexual swellings could have evolved as sexually selected traits whose attractiveness to males increases female fitness (e.g., Clutton-Brock & Harvey 1976; Nunn, 1999; Pagel, 1994). Throughout the 20th century, sexual skin color changes in females were described and analyzed in a variety of species, including macaques (e.g., Baulu, 1976; Bielert et al., 1976; Collings, 1926; Corner, 1932, 1935; Czaja et al., 1975; Hartman, 1928; Heape, 1896; Pocock, 1925; Tinklepaugh & Hartman, 1930; Zuckerman et al., 1938), gelada (Garrod, 1879; Matthews, 1956; Pocock, 1925), baboons (e.g., Altmann, 1973; Gillman & Gilbert, 1945, 1946, 1951; Pocock, 1925), mangabeys (e.g., Pocock, 1906), colobines (e.g., Pocock, 1935), and chimpanzees (e.g., Elder & Yerkes, 1936).

The 20th century also saw research on male sexual skin. As in research on females, most studies initially focused on physiology and ontogeny. Researchers linked the expression of darker sexual skin color with reproductive opportunities and the mating season (Gordon & Bernstein, 1973; Sade, 1964), described the development of colorful secondary sexual characteristics (Wickings & Dixson, 1992; Zuckerman et al., 1938), and linked the expression of these traits to hormone levels (both estrogen and testosterone; Vandenberg, 1965; Wickings & Dixson, 1992; Zuckerman et al., 1938; Zuckerman & Parkes, 1939). Noting the conspicuousness of **(p.103)** male sexual skin color, researchers reasoned that it may have a signaling function (Guthrie, 1970; Rowland, 1979; Wickler, 1967). Some suggested functions related to male rivalry and that male signals were products of intrasexual selection (e.g., Bercovitch, 1996), while others suggested more general social functions such as appeasement (e.g., Wickler, 1967). Descriptions of male sexual skin focused on a variety of species during the 20th century, including macaques (e.g., Zuckerman et al., 1938), baboons (Gordon & Bernstein, 1973; Kummer, 1968; Sade, 1964; Vandenberg, 1965; Zuckerman & Parkes, 1939), mandrills (e.g., Hill, 1970; Wickings & Dixson, 1992), drills (e.g., Zuckerman & Parkes, 1939), guenons (e.g., Bercovitch, 1996; Kingdon, 1980; Wickler, 1967), and langurs (e.g., Zuckerman & Parkes, 1939).

Overall, much of the early research on primate sexual skin coloration focused on proximate mechanisms, such as the role of hormones and development on color expression. Increasingly throughout the 20th century, however, researchers started to focus more on the ultimate function and comparative evolution of colorful primate traits and to undertake investigations of how sexual selection theory can explain the evolution of conspicuous coloration in primates.

Conceptual and Methodological Transitions

Over time, primate coloration has been studied using a variety of different approaches, with recent developments ushering in a new era of research on conspicuous coloration and sexual selection in primates. In Darwin's time, biologists generally amassed detailed descriptions of animal behaviors and morphologies, which were then used to infer their function and identify evolutionary trends. Early naturalists amassed wonderful descriptions of animal colors that contributed to the knowledge of their contemporaries and continue to captivate those interested in natural phenomena to this day.

In the early 20th century, biologists began to focus on experimental research and more precise measurements of animal behavior and morphology. While qualitative descriptions still occurred, there was a growing trend to quantify descriptions of animals and to test explicit predictions. Previous research, including that of Darwin, was criticized as being overly anthropomorphic, and backing up conclusions with numbers became paramount. Some researchers studying primate coloration began quantifying color change based on visual categorizations (e.g., Sade, 1964) or via comparisons with color cards (e.g., Bercovitch, 1996; Corner, 1932). **(p.104)** While these are relatively crude methods by modern standards, the transition to analyzing primate coloration based on quantifiable changes and comparisons was an important advancement in the field.

Eventually, biologists also began to conduct experiments analyzing primate colors that had been manipulated, allowing researchers to determine the effect of variations in a signal while controlling for all other potential factors. The first experimental assessment of primate coloration and sexual selection focused on the color of primate sexual swellings. Bielert, Girolami, and Jowell (1989) fitted female baboons with a model of a sexual swelling that was painted a variety of colors and measured resulting male sexual arousal. The red swelling yielded the highest male arousal, leading to the conclusion that sexual skin color is an important factor in female attractiveness to males when all other factors are held constant. Later studies have used experimental methods to investigate the use of a variety of colors exhibited by primates in both intrasexual competition (e.g., vervet monkey scrotal color; Gerald, 2001) and intersexual mate choice (e.g., rhesus macaque facial skin color; Dubuc et al., 2016; Higham et al., 2011; Waitt, Gerald, Little, & Kraiselburd, 2006; Waitt et al., 2003). Such experiments that directly test subjects' responses to visual stimuli are essential for understanding the functions of primate colors.

Recent times have seen an increase in research focused on conspicuous coloration and sexual selection in primates. The advent of digital photography provided researchers with a more accurate method of quantitatively measuring primate colors in a variety of settings (Stevens, Párraga, Cuthill, Partridge, & Troscianko, 2007), and information about the visual systems of primate species has allowed researchers to model colors as seen by their subjects (Stevens, Stoddard, & Higham, 2009) and take perceptually relevant measurements of color distances (e.g., units of "just noticeable differences"; Stern & Johnson, 2010). These new methods, along with a renewed interest in sexual selection throughout evolutionary biology, have spurred much additional research in modern times.

Recent Studies of Primate Coloration

Darwin's theory of sexual selection created the template for much of the modern research on primate colors. Current research questions are generally framed to assess whether conspicuous coloration primarily evolved under intrasexual or intersexual selection. This is often established by identifying the primary receivers of the signal and determining how they **(p.105)** respond to variation in the signal's expression. If the receivers are the same sex as the signaler, the signal has likely evolved under stronger intrasexual selection, whereas if the receivers are the opposite sex, the signal has likely evolved under stronger intersexual selection. It is probable that many signals evolved under both selective mechanisms, given that this distinction is Darwin's rather than the animals', but empirical studies typically separate the two. There have, however, been recent calls to integrate selective mechanisms when evaluating the form and strength of selection on sexual signals, as intrasexual and intersexual selection may reinforce or oppose one another (Hunt, Breuker, Sadowski, & Moore, 2009).

Recent methodological advances in digital photography have allowed coloration to be quantified (Stevens et al., 2009) and compared to social variables in captive, wild, and free-ranging primate populations. To test the alternative hypotheses that a colorful primate signal is under intrasexual versus intersexual selection, both observational and experimental approaches are undertaken and often complement one another. Observational approaches include assessing how variation in the signal relates to social status, mediates intrasexual agonistic interactions, and/or influences intersexual mating behavior. Experimental approaches include the looking-time paradigm, which uses photographic stimuli to assess attentional biases between the sexes (Winters, Dubuc, & Higham, 2015). Attentional biases can be due to both intimidation and attraction, making this a relevant paradigm for uncovering bias that results from male-male competition or female mate choice. Some studies have used both experimental and observational approaches by pairing captive individuals together in same-sex or opposite-sex pairs that express different signal intensities to understand how signal variation mediates dyadic social interactions (e.g., Gerald, 2003; Gerald, Ayala, Ruíz-Lambides, Waite, & Weiss, 2010).

Males of many primate taxa exhibit bright coloration on their face, hindquarters, genitals, or chest, which is highly unusual for mammals. Given the similarities in form to the colorful and elaborate ornaments of many male birds, these bright primate colors have been hypothesized to be a product of female mate choice (Clutton-Brock & McAuliffe, 2009). In contrast, recent research has shown that they generally function as “badges of status,” correlating strongly with social status, similar to most other male mammalian traits that have evolved under male–male competition (e.g., Emlen, 2014). Male mandrills (*Mandrillus sphinx*) are characterized by multicolored faces, rumps, and genitals; drills (*M. leucophaeus*) exhibit multicolored rumps and genitals and a red lower lip; crested macaques **(p.106)** (*Macaca nigra*) exhibit red scrotal coloration; gelada (*Theropithecus gelada*) exhibit red chest patches; vervet monkeys exhibit red, white, and blue genital coloration; and black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) exhibit red lips. In all of these species, both observational and experimental evidence show that coloration generally correlates with social status, such that males of higher dominance rank or those who hold one-male units express more intense coloration (mandrills: Renoult, Schaefer, Sallé, & Charpentier, 2011; Setchell & Wickings, 2005, drills: Marty, Higham, Gadsby, & Ross, 2009; crested macaques: Engelhardt, Neumann, Heistermann, & Perwitasari-Farajallah, 2008; gelada: Bergman, Ho, & Beehner, 2009; vervet monkeys: Cramer, 2012; snub-nosed monkeys: Grueter et al., 2015). This coloration is also responsive to changes in social status, as males rapidly change in color after the take-over of a high-ranking position (Bergman et al., 2009; Setchell & Dixson, 2001). These conspicuously colored signals appear to be important in mediating male–male interactions (e.g., Gerald, 2001), and there is limited evidence that they are attractive to females and influence female mating behaviors after controlling for male dominance rank (e.g., drills: Marty et al., 2009; vervet monkeys: Gerald et al., 2010). When a female preference for male coloration has been found (e.g., mandrills: Setchell, 2005), it is difficult to separate the effects of coloration and dominance on male attractiveness since dominance is so strongly correlated with coloration in these taxa. Therefore, it appears that intrasexual selection is generally the stronger selective pressure on the evolution of colorful male sexual signals in many primate species.

An interesting case of male coloration in primates that differs from this typical pattern is the rhesus macaque (*Macaca mulatta*). Rhesus macaques express covarying red coloration on their face, rump, and genitals (Higham, Pfefferle, Heistermann, Maestripieri, & Stevens, 2013) that intensifies in the mating season due to seasonal changes in testosterone (Baulu, 1976). Unlike in other primates studied, facial coloration does not correlate with dominance rank (Dubuc, Allen, Maestripieri, & Higham, 2014; Higham et al., 2013), and instead there is observational and experimental evidence that coloration is attractive to females (Dubuc, Allen et al., 2014; Dubuc et al., 2016; Waitt et al., 2003). Additionally, red ornamentation is heritable and influences fecundity; darker red males experience higher reproductive success when combined with high dominance rank (Dubuc, Winters et al., 2014). This evidence suggests that red ornamentation in male rhesus macaques is primarily under intersexual selection, which is unusual for a mammalian sexual signal. Despite this, male coloration may still mediate **(p.107)** male-male interactions. Adult males experimentally show an attentional bias toward dark red compared to pale pink males (Dubuc et al., 2016), and there is observational evidence that coloration differences may influence male dyadic agonism (Petersdorf et al., 2017), similar to the pattern seen in vervet monkeys (Gerald, 2001).

Conspicuous color signals are more common in primate males, but uniquely among mammals, females of many species also exhibit elaborate visual ornamentation. Significantly less work has focused on coloration in female sexual signals, particularly on the intrasexual and intersexual selective mechanisms. Most research on female color signals has been in relation to fertility advertisement. In some catarrhine primate taxa, intraindividual variation in facial coloration over time signals the fertile phase (e.g., rhesus macaques: Dubuc et al., 2009, Higham et al., 2010; Japanese macaques, *Macaca fuscata*: Fujita, Sugiura, Mitsunaga, & Shimizu, 2004). Whether this variation influences responses of conspecifics has only been assessed in rhesus macaques: males can discern intraindividual fertility differences in female facial coloration, although this ability increases with social familiarity (Higham et al., 2011). Fertility does not seem to be advertised in the coloration of other sexual signals examined, such as the sexual swellings of olive baboons, with swelling size cues seemingly more important in indicating the timing of the fertile phase (*Papio anubis*: Higham, MacLarnon, Ross, Heistermann, & Semple, 2008).

In addition to within individual variation, female coloration also varies between individuals. In rhesus macaques, female facial coloration is heritable and positively influences fecundity (Dubuc, Winters et al., 2014). Males show attentional biases toward images of redder females (Waitt et al., 2006), and females with redder faces reproduce at higher rates (Dubuc, Winters et al., 2014), suggesting that female facial coloration evolved under intersexual selection via male mate choice. More work on other species is needed to confirm how different sexual selection pressures have led to the evolution of female primate color ornamentation.

It is not yet clear what quality coloration may advertise in primates that opposite-sex individuals may find attractive. Sexual skin coloration is under proximate control of sex steroid hormones, and its expression is related to the degree of blood flow and oxygenation in the sexual skin (Changizi, Zhang, & Shimojo, 2006; Rhodes et al., 1997; Vandenberg, 1965). Coloration might therefore be an honest signal of condition (Folstad & Karter, 1992) or current health (Hamilton & Zuk, 1982); however, female facial coloration in some species does not appear to reflect body **(p.108)** condition (mandrills: Setchell, Wickings, & Knapp, 2006) or parasite load (Japanese macaques: Rigai et al., 2017).

On the whole, recent research on conspicuous coloration in primates has progressed extensively in recent years, and we now have a much greater understanding of how intrasexual and intersexual selection function in primates, the ways in which these selective dynamics make primates unique among mammals, and the underlying characteristics that may be signaled by primate colors. The Darwinian sexual selection framework has been essential for structuring research in this area and for understanding how and why primate colors are related to reproductive competition.

Future Directions

While the past decade has seen a surge of research in conspicuous coloration and sexual selection in primates, much work remains to be done, including assessments of specific color patterns in individual primate groups as well as broader trends across species. Primates are an extraordinarily colorful group, yet relatively few primate taxa have been the subject of quantitative analyses of color patterns that may be relevant in a mating context. For example, in a review of the evidence for mate choice based on color in primates, Higham and Winters (2016) identified 13 studies investigating the phenomenon in nine species: three lemurs, five cercopithecines (Old World monkeys), and one ape. Some entire branches of the primate phylogenetic tree have yet to be studied for such questions, including New World monkeys and the Asian colobines. This is particularly noteworthy because these groups contain some primates with extremely interesting appearances, such as the emperor tamarin (*Saguinus imperator*) and the golden snub-nosed monkey (*Rhinopithecus roxellana*). Studies investigating how sexual selection has influenced the colors and patterns displayed by species in these groups are ripe for the taking.

In addition to studies seeking to explain species-specific coloration, additional work should focus on identifying evolutionary trends based on comparisons across species. In 2008, Bradley and Mundy published an excellent review of primate coloration in which they evaluated the selective forces likely to have helped shape primate diversity, including sexual selection. They pointed to many unanswered questions that could be addressed using comparative analyses assessing traits and species characteristics across primate species. These include the fascinating phenomena of sexual dichromatism—whereby females and males of the same species (**p.109**) are differently colored, and of natal coat colors—whereby the infants of primate species show coats that are conspicuous orange and yellow colors that contrast strikingly with the darker fur of their parents. However, to date few of these interspecific studies have been undertaken using modern methods with detailed measurements of primate colors and appropriate statistical controls for the phylogenetic relationships between species. In part, the lack of broader comparative analyses of the role of sexual selection in primate coloration is due to the lack of available data from many species. Many primate colors likely to be involved in sexual signaling are located on the skin. These colors do not preserve post mortem and therefore cannot be analyzed based on museum specimens. It is notable that recent comparative analyses of primate coloration (e.g., Kamilar & Bradley, 2011a, 2011b; Winters, Kamilar, Webster, Bradley, & Higham, 2014) have focused on the evolution of pelage colors with respect to crypsis and predator avoidance (i.e., natural selection). To understand why and how primate colors have evolved by sexual selection, we need to amass more information about the diversity of primate coloration, including quantitative descriptions (e.g., spectral measurements) of primate skin colors as well as analyses of functionality (e.g., determining that a color patch in a given species has evolved via mate choice).

Rather than always studying a single color patch in isolation, research should also focus on the structures and patterns associated with primate colors, as well as how different patches combine to create a total visual phenotype (Allen & Higham, 2013). Contrasting colors, patterns, and optical effects created by primate colors could be under intrasexual and/or intersexual selection, but this has not yet been tested. New methods for analyzing animal patterns (e.g., Stoddard, Kilner, & Town, 2014; Troscianko & Stevens, 2015; Tylor, Gilbert, & Reader, 2013) could be applied to the analysis of primate color patterns to test this hypothesis.

Conclusion: Darwin's Roadmap to Primate Coloration

Darwin was fascinated by primate coloration. He explicitly began asking questions about how and why colors had evolved, posing questions about their functions and underlying mechanism. His insights into sexual selection gave researchers a roadmap to follow for investigating primate colors, which researchers of the topic have used to frame their studies and research questions. As such, the study of primate coloration can be held up as an exemplar for how Darwinian thinking framed and continues to shape **(p.110)** academic study in the 21st century. Colors that appear to have evolved via intrasexual and intersexual selection have been identified in a variety of primate species, and it is clear that primates are an excellent group in which to study sexual selection in mammals. In many ways, research on conspicuous coloration and sexual selection in primates has come full circle. Darwin used colorful primate traits as key examples when initially articulating his theory of sexual selection, but research on primate coloration and sexual selection was rare for decades afterward. Renewed interest in this topic as well as developments in methods and technology making it easier to quantify primate colors has led to a surge of research in this area in recent times. This reflects sexual selection research returning to its roots, as researchers in the 21st century provide the required evidence that Darwin's ideas about the colors of monkeys were right all along.

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