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# 24 Color and mate choice in non-human animals

James P. Higham and Sandra Winters

## Introduction

The role of color in animal mate-choice decisions has been a source of interest and speculation at least since the dawn of modern evolutionary theory. Darwin wrote extensively about coloration in his primary work on sexual selection, *The Descent of Man, and Selection in Relation to Sex*, published in 1871. Darwin also wrote an article on the topic that was published in the journal *Nature* in 1876, entitled "Sexual selection in relation to monkeys." He opened his paper with the following words (p. 18):

In the discussion on Sexual Selection in my 'Descent of Man', no case interested and perplexed me so much as the brightly-coloured hinder ends and adjoining parts of certain monkeys. As these parts are more brightly coloured in one sex than the other, and as they become more brilliant during the season of love, I concluded that the colours had been gained as a sexual attraction.

Darwin's speculations on the role of coloration in primate mate choice would not begin to be empirically tested for more than a century, although naturalists continued to document the colors formed and exhibited by different taxa (e.g., birds; Newton, 1896). The study of the role of animal coloration in mate choice in modern times began with the advent of behavioral ecology. Here, behavioral observations of animals started to be considered within a stronger evolutionary framework than had been typical of the ethological tradition. Further, though behavioral ecology might be associated with the study of behavior, it has really had a much broader focus – integrating the study

of behavior with that of hard- and soft-tissue morphologies, physiology, genetics, and the social and ecological factors that influence their evolution. As such, pelage and skin coloration have been common topics of study for behavioral ecologists, and this discipline has produced a vast number of studies on coloration and its role in mate choice. However, before we go on to review this work, we will first consider the role of sexual selection in determining the types and extent of mate choice in different taxonomic groups.

## Sexual selection mechanisms and mate choice

There is a fundamental difference in reproductive potential between males and females that has important implications for sexual selection. Female reproduction is primarily limited by physical resources, such as food availability, while male reproduction is primarily limited by reproductive resources – i.e., females (Bateman, 1948; Trivers, 1972). This is because females are the sex that invests by far the most resources in rearing young, while, in many animal groups, males contribute little other than sperm. These fundamental differences between males and females and their implications for mechanisms of sexual selection were summarized by Darwin (1871, ch. 21) as follows:

The sexual struggle is of two kinds: in the one it is between the individuals of the same sex, *generally the males*, in order to drive away or kill their rivals, the females remaining passive; while in the other,

the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, *generally the females*, which no longer remain passive, but select the more agreeable partners. (our italicization)

Usually, one of these two mechanisms comes to predominate, such that it is under circumstances of lower direct male–male competition that we expect more female mate choice. Different taxa experience different mechanisms of sexual selection at different strengths, and it is important to consider this when evaluating coloration and mate choice among different animal groups. For example, mammals typically show strong direct male–male competition, a mechanism of intrasexual selection. This leads to the evolution of weaponry, such as long canines, horns, and antlers (Clutton-Brock and McAuliffe, 2009; Emlen, 2008). Males who are successful in fighting then take the spoils – the females – and there may often be little scope for females to exert direct mate choice. In contrast, in birds, direct male–male competition over females is rare – males rarely have violent and costly fights over females. Instead, males attract females with colorful ornaments, such as the peacock's tail, and the vivid colors of the many species of bird of paradise (Hill and McGraw, 2006). Consistent with this increased role for female mate choice in determining male mating success, male birds rarely exhibit weapons (Clutton-Brock and McAuliffe, 2009). This distinction between birds and mammals was noted by Darwin (1871, ch. 21):

I presume that no supporter of the principle of sexual selection believes that the females select particular points of beauty in the males; they are merely excited or attracted in a greater degree by one male than by another, and this seems often to depend, *especially with birds*, on brilliant colouring. (our italicization)

Understanding these broad taxonomic differences in sexual selection mechanisms is crucial for understanding the likelihood that ornaments, and hence colors, might be utilized in mate choice in different groups. However, other factors also influence comparative variation in the exhibition of color, and we will consider these next.

## Colors shown by different taxa

Before we review the evidence for the use of color in mate choice for different taxa, it is important first to consider the colors exhibited by animals. Several different considerations come into play, all of which may influence or limit the colors that a species or group of species may show:

(1) *Color production* – this involves the mechanisms by which colors are synthesized and displayed. Animal colors can be produced via the use of pigments, which may be either synthesized in the body or obtained from food sources, or through structural colors, which are created by the physical structure of a surface, or both. The likelihood of a species displaying a specific color can be influenced by the ease with which that color can be produced. For example, mammalian hair colors are derived from yellow/red pheomelanin and brown/black eumelanin pigments, synthesized through the melanocyte pigment pathway (Slominski et al., 2004). This might make the use of red colors more likely, while potentially limiting the exhibition of blues and purples (Bradley and Mundy, 2008). The color of mammalian blood is also red, and red skin coloration with roles in dominance or mate-choice communication that is known to be linked to underlying blood flow is exhibited by many primates, including humans (Dixson, 2012). Despite these potential limitations on color expression, many domesticated breeds of mammals exhibit bluish colors, formed from a mixture of white and pigmented hairs via the roan or grullo phenotype (Seitz et al., 1999).

Similarly, blue skin colors are exhibited in some primate species by the presence of subdermal melanin (Dixson, 2012). The exhibition of blue colors in mammals is therefore possible, even if it is rare. With the exception of mammalian hair, the production of colors is less limited in most vertebrates because they incorporate dietary carotenoids and other pigments into their observed coloration (McGraw, 2006a). The incorporation of these ingested pigments primarily allows for the increased expression of vibrant reds, oranges, and yellows (McGraw, 2006a, 2006b). In most animals, lower wavelength colors (i.e., greens, blues, purples) are produced by microscopic structures on the surface of the body. Structural colors tend to be easier to produce in some tissues, such as feathers, scales, and insect wings, and that may be why these colors are more common in certain taxa (Ghiradella, 1991; Prum, 2006). Particular emphasis has been placed on the mechanisms influencing bird coloration. Birds are an extremely colorful group, and exhibit colors ranging from dark red to ultraviolet (UV). Nonetheless, despite the wide range of colors that are exhibited by birds, only a small area of the total color space that birds can theoretically see is used, and vast areas of avian color space remain unused (Stoddard and Prum, 2011). It seems likely therefore that other factors also influence the total gamut of color that birds show. Overall, differences between color-production mechanisms across taxa are likely to influence the colors each group is likely to display.

(2) *Visual systems* – we should expect the range of colors shown by a taxon to be related to the visual systems found within that group, and found in the predators of that group. Birds are tetrachromats, and detect colors not only at the wavelengths that humans can see, but also at very short wavelengths through the presence of UV or SUV retinal cones (Lind et al., 2013; Osorio and Vorobyev, 2005) and lens/cornea that transmit UV color (Cuthill et al., 2000). Consistent with this, birds make extensive use of UV colors in their mate choice signals (Hill and McGraw, 2006; Stevens and Cuthill, 2007). Indeed, it has been suggested that predation of birds by dichromatic carnivores such as cats has led birds to use UV colors extensively in conspecific communication, precisely because such wavelengths are not perceptible to those predator types (Guilford and Harvey, 1998; but see Stevens and Cuthill, 2007). Most mammals are dichromatic and cannot distinguish colors at medium to long wavelengths (greens to reds), and red coloration is very rare among this group. An exception is found among primates, where many species are uniform trichromats (catarrhines and howler monkeys) or have polymorphic vision, with some females exhibiting trichromacy (most platyrrhines and many diurnal lemurs). Many of these species exhibit red colors consistent with their ability to perceive these colors. Similar to the avian example, the use of red colors may be because such colors cannot be distinguished from green backgrounds by dichromatic predators such as carnivores (Sumner and Mollen, 2003; Winters et al., 2014). Moreover, there is good evidence in some taxa for spectral tuning of signals to visual systems. Examples include many species of fireflies, where there is often a close match between the spectrum of the bioluminescent signals each species emits, and the corresponding spectral sensitivity of the photopigments possessed (Lall, 1980; Lall et al., 2010).

(3) *The environment* – this includes both the composition and availability of the lighting environment, and the background environments, such as the colors of forests. Light

travels in straight lines such that features of the environment, from hills to trees, prevent visual transmission of color signals. Weather conditions that affect the air, such as fog and rain, can also prevent good visual conditions. For aquatic animals, water turbidity is crucial. Cichlid fish found in more turbid water are less colorful than those found in clear water (Seehausen et al., 1997), and both coloration and courtship behavior of three-spined sticklebacks are affected by increased turbidity (Wong et al., 2007). The background colors in which species find themselves also affect the colors selected, including those for camouflage and mimicry (Stevens et al., Chapter 17, in this volume), but also potentially for signals used for mate choice. The effects of the background environment on coloration may be determined by interactions with visual systems. For example, recent evidence suggests that the colors that primates show are extremely well matched to forest backgrounds in the eyes of dichromatic predators, but are more chromatically contrasting to backgrounds in the eyes of conspecifics (Winters et al., 2014).

Together, these different factors will all influence the likelihood of individual taxa and species exhibiting particular colors – a clear prerequisite for their use in mate choice. The use of coloration in mate choice may occur following initial selection of particular colors for other purposes (e.g., the color of blood in primates; Changizi et al., 2006), may develop from pre-existing sensory biases (e.g., a preference for colorful fruits or leaves important in diet; Arak and Enquiest, 1993), or may be driven by mate choice from the outset.

# Color and mate choice in non-humans

In choosing which literature to present in this chapter, we have had to be selective. The first issue is to decide what constitutes mate choice. There is a great deal of literature showing that colors may be used in aggressive interactions or dominance disputes between males, with males successful in these conflicts obtaining the majority of reproductive opportunities. Such signals are likely to have evolved from processes of intrasexual selection (male–male competition) rather than from intersexual selection and mate choice. Similarly, there are many cases where males of high social status and/or quality have been shown both to be colorful and to have high reproductive output. Again, it is not clear whether this is because colorful males are more attractive to females *per se*. We have restricted our chapter to literature where mate choice has been measured directly – for example, by the measurement of the frequency of female approaches or presentations to males.

## Color and mate choice in non-primates

Though it would be impossible to summarize all the literature on the use of colors in mate choice in non-primates in a subsection of one book chapter, we have provided many examples in Table 24.1. This is meant to be representative rather than exhaustive, but is taxonomically broad. Here we will briefly summarize the state of evidence for the role of color in mate choice across many major animal taxa.

A number of studies have assessed the impact of color on mate choice in insects, particularly in butterflies and damselflies. Various colors have been associated with mate choice in this group, including UV reflectance, which is perceptible by most insects (Briscoe and Chittka, 2001). In butterflies, mate choice has been related to many different colors across different species, with both males and females generally preferring brighter or more species-typical wing or thorax colors (Table 24.1). In some cases, however, mate choice based on color is restricted to one sex; for example, in the pipevine swallowtail (*Battus philenor*), females prefer males whose dorsal

Table 24.1 *A sample of studies assessing intraspecific mate choice based on color in non-primate species*

| Species | Common name | Sex tested | Body region | Colors analyzed | Evidence for mate choice? | Preferences | References |
|---|---|---|---|---|---|---|---|
| **Insects** | | | | | | | |
| *Argia apicalis* | Blue-fronted dancer | Male | Abdomen, thorax | Brown, gray/black, turquoise | Yes | Brown over gray/black or turquoise | Bick and Bick, 1965 |
| *Battus philenor* | Pipevine swallowtail | Male | Whole body | Blue | No | Males do not use visual cues to recognize females | Rutowski and Rajyaguru, 2013 |
| *Battus philenor* | Pipevine swallowtail | Female | Dorsal region | Blue iridescence | Yes | Natural blue iridescence over that which had been blacked out | Rutowski and Rajyaguru, 2013 |
| *Colias philodice eriphyle* | Clouded sulfur butterfly | Male | Wings | Melanization (yellow to black) | Yes | Yellower models | Ellers and Boggs, 2003 |
| *Enallagma civile* | Familiar bluet damselfly | Male | Abdomen | Blue (andromorph), green/tan (gynomorph), blue/green (gynomorph) | Mixed results | Based on previous experience | Fincke et al., 2007 |
| *Eurema hecabe* | Large grass yellow butterfly | Female | Whole body | UV iridescence | Yes | Conditions allowing UV perception | Kemp, 2008 |
| *Hypolimnas bolina* | Great eggfly | Female | Dorsal region | Blue/UV iridescence | Yes | Natural blue/UV iridescence over that which had been blacked out or dulled | Kemp, 2007 |
| *Ischnura elegans* | Blue-tailed damselfly | Male | Abdomen | Blue (andromorph), brown/green (gynomorph) | Mixed results | Live gynochrome over androchrome females; equally (highly) attracted to dead female models of all color morphs | Andres et al., 2002 |
| *Ischnura elegans* | Blue-tailed damselfly | Male | Abdomen | Blue (andromorph), brown/green (gynomorph) | No | Depend on frequency and recent exposure | van Gossum et al., 1999, 2001 |
| *Pieris occidentalis* | Western white butterfly | Male | Marginal forewing | Black/gray (melanization) | Yes | Intact males over those whose marginal forewing melanin characters were removed (whitened) | Wiernasz, 1989 |
| *Pieris occidentalis* | Western white butterfly | Female | Dorsal wing | Black/gray (melanization) | Yes | Typical melanin pattern over heavy melanation | Wiernasz, 1995 |
| *Pieris protodice* | Checkered white butterfly | Female | Dorsal wing | Black/gray (melanization) | Yes | Typical melanin pattern over heavy melanation | Wiernasz, 1995 |
| *Pieris rapae* | Cabbage white butterfly | Female | Dorsal wing | Blue/green, UV | Yes | Brighter blue/green color, less bright UV color | Morehouse and Rutwski, 2010 |
| **Crustaceans** | | | | | | | |
| *Callinectes sapidus* | Blue crab | Male | Claw | Red, orange, luminance | Yes | Red over orange | Baldwin and Johnsen, 2012 |
| *Callinectes sapidus* | Blue crab | Male | Claw dactyls | Red, black, white | Yes | Red over white or back | Baldwin and Johnsen, 2009 |
| *Uca mjoebergi* | Fiddler crab | Female | Claw | Yellow, gray | Yes | Yellow over gray (regardless of intensity) | Detto, 2007 |
| *Uca mjoebergi* | Fiddler crab | Female | Whole body | UV | Yes | UV reflectance not blocked | Detto and Blackwell, 2009 |
| **Arachnids** | | | | | | | |
| *Cosmophasis umbratica* | Jumping spider | Male | Palps | UV-excited green fluorescence | Yes | Natural UV-induced green fluorescence over blocked | Lim et al., 2007a |
| *Cosmophasis umbratica* | Jumping spider | Female | Face and body | UV | Yes | UV reflectance not blocked | Lim et al., 2007a |
| *Cosmophasis umbratica* | Jumping spider | Female | Full body | UV | Yes | UV chroma available over only UV luminance or no UV available | Lim et al., 2007b |
| *Habronattus pyrrithrix* | Jumping spider | Female | Face (red), leg (green) | Red, green, black | Mixed results | Natural sunlight: red over black (face); artificial light: no preference (face and legs) | Taylor and McGraw, 2013 |
| *Maevia inclemens* | Jumping spider | Female | Body and legs | Black body and white legs, black and white striped body and legs | No | No preference (once other factors were taken into account) | Clark and Uetz, 1991 |
| *Phintella vittata* | Jumping spider | Female | Whole body | UV | Yes | UV reflectance not blocked | Li et al., 2008 |
| *Schizocosa uetzi* | Wolf spider | Female | Legs | Black, brown | Yes | Based on previous experience | Hebets, 2003 |

Table 24.1 *(cont.)*

| Species | Common name | Sex tested | Body region | Colors analyzed | Evidence for mate choice? | Preferences | References |
|---------|-------------|------------|-------------|-----------------|---------------------------|-------------|------------|
| **Cephalopods** | | | | | | | |
| *Sepia officinalis* | Common cuttlefish | Female | Face (during zebra display) | Gray/black | No | No preference based on relative darkness | Boal, 1997 |
| **Fish** | | | | | | | |
| *Gasterosteus aculeatus* | Three-spined stickleback | Female | Throat | Red | Yes | More intense color | Bakker and Mundwiler, 1994; McLennan and McPhail, 1990; Milinski and Bakker, 1990; Semler, 1971 |
| *Gasterosteus aculeatus* | Three-spined stickleback | Female | Belly, whole body | Red, green, tan, yellow | Yes | Red belly over green belly, whole-body tan, and whole-body red; yellow belly over red belly; no preference for whole-body red versus tan | Baube et al., 1995 |
| *Gasterosteus aculeatus* | Three-spined stickleback | Female | Whole body | UV | Yes | UV chroma not blocked | Rick et al., 2006 |
| *Gasterosteus aculeatus* | Three-spined stickleback | Female | Anterio-ventral regions | Red, black | Yes | Red or black over dull coloration | McKinnon, 1995 |
| *Gobiusculus flavescens* | Two-spotted goby | Male | Belly | Yellow/orange | Yes | Colorful over dull coloration | Amundsen and Forsgren, 2001 |
| *Neochromis omnicaeruleus* | Lake Victoria cichlid | Female | Overall color morph | Yellow/brown, orange, white, black | Mixed results | Individual differences in preferences | Pierotti et al., 2009 |
| *Pelvicachromis taeniatus* | African cichlid | Female | Ventral belly | Purple | Yes | Larger colored region | Baldauf et al., 2011 |
| *Poecilia latipinna* | Sailfin molly | Female | Whole body | UV | Yes | UV reflectance not blocked | Palmer and Hankison, 2012 |
| *Poecilia reticulata* | Guppy | Female | Torso and tail | Red, orange, yellow, blue, black, UV, iridescence, overall brightness | Yes | Many studies have found preferences for brighter colors, especially in red/orange | Brown and Johnson, 2002; Houde, 1997 (and references therein; see table on p. 48); Kodric-Smith et al., 2002 |
| *Poecilia reticulata* | Guppy | Female | Torso and tail | UV | No | No preference based on level of UV reflection | White et al., 2003 |
| *Xiphophorus nigrensis* | Swordtail | Female | Whole body | UV | Yes | UV not blocked | Cummings et al., 2003, 2006 |
| *Xiphophorus pygmaeus* | Pygmy swordtail | Female | Body | Blue, gold | Yes | Blue over gold (two out of three populations) | Kingston et al., 2003 |
| **Amphibians** | | | | | | | |
| *Dendrobates pumilio* | Strawberry poison-dart frog | Female | Whole body | Orange, green | Yes | Prefer own morph when color information available | Summers et al., 1999 |
| *Dendrobates pumilio* | Strawberry poison-dart frog | Female | Whole body | Yellow/green with black spots, red orange with few/no spots | Yes | Prefer own morph when color information available | Reynolds and Fitzpatrick, 2007 |
| *Dendrobates pumilio* | Strawberry poison-dart frog | Female | Dorsal reflectance | Brightness | Yes | Brighter males | Maan and Cummings, 2009 |
| *Hyla arborea* | European tree frog | Female | Throat sac | Red/orange, luminance | Yes | More colorful (increased chroma, decreased luminance) over less colorful | Gomez et al., 2009 |
| *Hyla arborea* | European tree frog | Female | Throat sac | Red/orange | Yes | Dark red over light orange; no difference between light red and dark orange | Gomez et al., 2010 |
| *Scaphiopus couchii* | Spadefoot toad | Female | Dorsal body | Yellow/green | Yes | Bright over dull coloration | Vasquez and Pfenning, 2007 |
| **Reptiles** | | | | | | | |
| *Anolis carolinensis* | Anole | Female | Dewlap | Red, green | Yes | Red over green | Sigmund, 1983 |

Table 24.1 *(cont.)*

| Species | Common name | Sex tested | Body region | Colors analyzed | Evidence for mate choice? | Preferences | References |
|---|---|---|---|---|---|---|---|
| *Chamaelo chamaeleon* | Mediterranean chameleon | Male | Body | Yellow | Yes | Yellow spots over no spots | Cuadrado, 1998 |
| *Crotaphytus collaris* | Collared lizard | Male | Torso, head | Orange | Yes | Orange spots over brown spots | Baird, 2004 |
| *Crotaphytus collaris* | Collared lizard | Female | Whole body | Subjective brightness | Mixed results | Brighter males in only some populations | Baird et al., 1997 |
| *Ctenophorus ornatus* | Agamid lizard | Male | Throat | UV | Yes | Higher chroma | LeBas and Marshall, 2000 |
| *Eumeces laticeps* | Broad-headed skink | Female | Head | Orange, brown | No | No preference | Cooper and Vitt, 1993 |
| *Lacerta viridis* | European green lizard | Female | Throat | UV | Yes | UV reflectance not blocked | Bajer et al., 2010 |
| *Microlophus occipitalis* | Knobbed Pacific iguana | Male | Throat | Red, white | Yes | White over red | Watkins, 1997 |
| *Pogona vitticeps* | Inland bearded dragon | Female | Beard | Dark black, light gray | No | No preference | Lane, 2013 |
| *Sauromalus obesus* | Chuckwalla | Female | Torso and tail | Orange, yellow | Mixed results | Brighter males (two out of three populations). Local morph over others (one out of three populations) | Kwiatkowski and Sullivan, 2002 |
| *Sauromalus obesus* | Chuckwalla | Female | Torso and tail | Orange, yellow | Mixed results | Local morph over others (one out of three populations) | Kwiatkowski and Sullivan, 2002 |
| *Urosaurus ornatus* | Ornate tree lizard | Female | Throat | Contrast between central patch (usually blue/green) and surrounding color (usually orange) | No | No preference | Hamilton and Sullivan, 2005 |
| **Birds** | | | | | | | |
| *Agelaius phoeniceus* | Red-winged blackbird | Male | Epaulet, chin | Red/orange | No | No preference for bright versus dull | Muma and Weatherhead, 1989 |
| *Aptenodytes patagonicus* | King penguin | Male | Auricular patches, breast | Yellow, white | No | No preference | Pincemy et al., 2009 |
| *Aptenodytes patagonicus* | King penguin | Female | Auricular patches, breast | Yellow, white | Yes | Yellow over white | Pincemy et al., 2009 |
| *Callipepla gambelii* | Gambel's quail | Female | Belly | Brown, white | No | No preference | Hagelin and Ligon, 2001 |
| *Callipepla gambelii* | Gambel's quail | Female | Head | Red/brown, gray | No | No preference | Hagelin and Ligon, 2001 |
| *Callipepla squamata* | Scaled quail | Female | Belly | Brown, white | No | No preference | Hagelin and Ligon, 2001 |
| *Carpodacus mexicanus* | House finch | Male | Plumage | Red to yellow | Yes | Redder plumage | Hill, 1993 |
| *Carpodacus mexicanus* | House finch | Female | Plumage | Red to yellow | Yes | Redder plumage | Hill, 1990, 1991; Toomey and McGraw, 2012 |
| *Euplectes ardens* | Red-collared widowbird | Female | Collar | Red | No | No preference | Pryke et al., 2001 |
| *Gallus gallus* | Red junglefowl | Female | Plumage | Red/orange, silver, brown | No | No preference | Ligon and Zwartjes, 1995 |
| *Gallus gallus* | Red junglefowl | Female | Comb, iris, hackle, head, saddle | Red, yellow | Yes | Brighter and/or darker red and yellow colors in various body regions | Zuk et al., 1990 |
| *Junco hyemalis* | Dark-eyed junco | Female | Tail | White | Yes | Experimentally enhanced white | Hill et al., 1999 |
| *Parus caeruleus* | Blue tit | Male | Whole body | UV reflectance | Yes | UV reflectance not blocked | Hunt et al., 1999 |
| *Parus caeruleus* | Blue tit | Female | Whole body | UV reflectance | Yes | UV reflectance not blocked | Hunt et al., 1999 |
| *Patagioenas* spp. | Pigeon | Male | Plumage | Blue, red | Yes | Blue over red | Burley, 1981 |
| *Patagioenas* spp. | Pigeon | Female | Plumage | Blue, red | Yes | Blue over red | Burley, 1981 |

Table 24.1 *(cont.)*

| Species | Common name | Sex tested | Body region | Colors analyzed | Evidence for mate choice? | Preferences | References |
|---|---|---|---|---|---|---|---|
| *Sula nebouxii* | Blue-footed booby | Male | Foot | Blue | Yes | Natural over modified (dull) color | Torres and Velando, 2005 |
| *Sula nebouxii* | Blue-footed booby | Female | Foot | Blue | Yes | Natural over modified (dull) color | Torres and Velando, 2003 |
| *Taeniopygia guttata* | Zebra finch | Male | Bill | Red/orange | Yes | Colors in the middle of the species range | Burley and Coopersmith, 1987 |
| *Taeniopygia guttata* | Zebra finch | Female | Bill | Red/orange, green | Yes | Bright red over light red; light red over green | Burley and Coopersmith, 1987 |
| *Taeniopygia guttata* | Zebra finch | Female | Bill | Red/orange | No | No preference (after controlling for song characteristics) | Collins et al., 1994 |
| *Taeniopygia guttata* | Zebra finch | Male | Leg band | Red, orange, blue, green, pink, black | Yes | Preferred red, black pink; neutral towards orange; avoided blue, green | Burley et al., 1982 |
| *Taeniopygia guttata* | Zebra finch | Female | Leg band | Red, orange, blue, green, pink, black | Yes | Preferred red; neutral towards orange, pink, black; avoided blue, green | Burley et al., 1982 |
| *Taeniopygia guttata* | Zebra finch | Female | Whole body | UV | Yes | UV reflectance not blocked | Bennett et al., 1996 |
| **Mammals** | | | | | | | |
| *Panthera leo* | African lion | Female | Mane | Black/yellow | Yes | Darker manes | West and Packer, 2002 |

blue iridescence is intact over those for which this region has been blacked out, but males appear to use chemical, rather than visual, cues to identify females. Damselflies are a particularly interesting group in which to study visual signals, because in many species there are multiple visually distinct female morphs. In many cases, some female morphs mimic male coloration, potentially to reduce harassment from males (van Gossum et al., 2001). Evidence for male preference of different color morphs is mixed – some studies have found preferences for gyno-morph females (i.e., those not mimicking males) (Andres et al., 2002), but others have found evidence for frequency-dependent preferences (van Gossum et al., 1999, 2001) or preferences based on past experience (Fincke et al., 2007).

In Crustacea, mate choice has primarily been assessed with respect to the color of crabs' claws. Male blue crabs (*Callinectes sapidus*) have been shown to prefer red claws in females (Baldwin and Johnsen, 2009, 2012), and female fiddler crabs (*Uca mjoebergi*) have been shown to prefer yellow over gray claws (Detto, 2007). Consistent with a recent emphasis on assessing animal signals not perceptible to humans, female fiddler crabs have also been shown to demonstrate preferences for males exhibiting natural UV reflectance over those whose UV reflectance has been blocked (Detto and Blackwell, 2009).

The role of color in mate choice in arachnids has primarily been studied in the jumping spider (*Cosmophasis umbratica*). UV-related signals appear to be particularly important in this group, with females preferring males whose UV reflectance has not been blocked (Li et al., 2008; Lim et al., 2007a, 2007b). Female jumping spiders do not exhibit UV reflectance, but they do display green fluorescence that is stimulated by UV light; males prefer fluorescent females, and therefore the presence of UV light is important to both sexes. In addition to UV signals, female jumping spiders also prefer males with red over black faces. However, this preference is only exhibited in natural sunlight, highlighting the importance of environmental conditions and experimental design in mate-choice studies (Taylor and McGraw, 2013).

Although a very colorful group, cephalopods have not been subject to much research on color and mate choice. In cuttlefish (*Sepia officinalis*), males engage in a "zebra display," in which their facial regions darken during courtship; however, thus far, there is no evidence that females prefer males based on the relative darkness of their displays (Boal, 1997). Given the ability of cephalopods to change their color phenotype rapidly (Hanlon and Messenger, 1996), more research is needed.

A good deal of research has focused on color and mate choice in fish. Numerous studies have been conducted in guppies (*Poecilia reticulata*), and female guppies have been shown to prefer brighter-colored males. A majority of studies have focused on red or orange coloration, but females have also been shown to prefer brighter yellow, blue, black, UV, iridescence, and overall color brightness (Houde, 1997; Kodric-Brown and Johnson, 2002; Smith et al., 2002; but see White et al., 2003). The three-spined stickleback (*Gasterosteus aculeatus*) has also been studied extensively. In many populations, males develop conspicuous red throat coloration during the mating season, and females prefer males with more intense coloration (Bakker and Mundwiler, 1994; McLennan and McPhail, 1990; Milinski and Bakker, 1990; Semler, 1971). In some cases female preferences have also been found for brighter yellow (Baube et al., 1995), black (McKinnon, 1995), and UV (Rick et al., 2006) coloration in this species. Female color preferences have also been found in other fish species, such as a preference for males with UV reflectance in sailfin mollies (*Poecilia latipinna*; Palmer and Hankison, 2012) and swordtails (*Xiphophorus nigrensis*; Cummings et al., 2003, 2006), blue over gold males in pygmy swordtails (*Xiphophorus jpygmaeus*; Kingston et al., 2003),

and brighter yellow-orange bellies in two-spotted gobies (*Gobiusculus flavescens*; Amundsen and Forsgren, 2001). In cichlids, a number of studies have assessed how color has influenced speciation in this group (e.g., Maan et al., 2006). Intraspecific mate-choice preferences have also been identified, however, such as a female preference for larger purple regions in the belly in African cichlids (*Pelvicachromis taeniatus*; Baldauf et al., 2011).

Amphibians are a strikingly colorful group, and this coloration has been studied in many cases with respect to aposematism (Cott, 1940), or the signaling of toxicity to potential predators (Rudh and Qvarnström, 2013). In at least some cases, aposematic signals may be under sexual selection, and female strawberry poison-dart frogs (*Dendrobates pumilio*) have been found to prefer more brightly colored males (Maan and Cummings, 2009), as well as males of their own local color morph (Reynolds and Fitzpatrick, 2007; Summers et al., 1999). Females exhibit preferences for red over orange throat sacs in European tree frogs (*Hyla arborea*; Gomez et al., 2009, 2010) and bright over dull yellow coloration in spadefoot toads (*Scaphiopus couchii*; Vasquez and Pfenning, 2007).

In reptiles, males and females of multiple species have been shown to exhibit preferences for certain colors or for generally brighter mates. Generally preferred colors include red, orange, and yellow (e.g., Baird, 2004; Cuadrado, 1998; Kwiatkowski and Sullivan, 2002; Sigmund, 1983); however, other preferences have also been documented, such as a male preference for white over red throats in knobbed Pacific iguanas (*Microlophus occipitalis*; Watkins, 1997) and a preference for individuals exhibiting UV reflectance in male agamid lizards (*Ctenophorus ornatus*; LeBas and Marshall, 2000) and female European green lizards (*Lacerta viridis*; Bajer et al., 2010). There have also been a number of studies that found no evidence for mate choice based on coloration in reptiles (e.g., Cooper and

Vitt, 1993; Hamilton and Sullivan, 2005; Lane, 2013), suggesting that other mechanisms of selection for conspicuous coloration may be important in this group.

Among mammals, evidence for mate choice based on color is relatively lacking. Most mammals have dichromatic vision (Jacobs, 1993), and are consequently able to perceive fewer colors than many other animals. Mate choice in this group is therefore probably based primarily on other characteristics (for a discussion of female mate choice in mammals, see Clutton-Brock and McAuliffe, 2009). The major exception to this is the primates, discussed further below. Apart from primates, there is also evidence for mate choice based on mane color in lions; female lions usually mate with the darkest maned lion in the group, and preferentially approach models of male lions with darker manes (West and Packer, 2002).

Perhaps the largest group of animals studied with respect to coloration and mate choice are the birds (class: Aves). Extensive research has analyzed the role of many different colors in a variety of bird species. On the whole, color appears to play a role in mate choice for both sexes in a number of bird species. Preferences have been documented for brighter versions of a variety of different colors, such as redder plumage in male (Hill, 1993) and female (Hill, 1990, 1991; Toomey and McGraw, 2012) house finches (*Carpodacus mexicanus*) and female red junglefowl (*Gallus gallus*; Zuk et al., 1990; but see Ligon and Zwartjes, 1995), redder bills in male and female zebra finches (*Taeniopygia guttata*; Burley and Coopersmith, 1987; but see Collins et al., 1994), and deeper-blue feet in male and female blue-footed boobies (*Sula nebouxii*; Torres and Velando, 2003). Some species have also demonstrated a preference for one color over another, such as a preference for yellow over white auricular and breast patches in female king penguins (*Aptenodytes patagonicus*; Pincemy et al., 2009) or blue over red plumage in male and female pigeons (*Patagioenas* spp.;

Burley, 1981). Multiple species have also demonstrated a preference for mates whose UV reflectance is visible over those behind UV-blocking filters (e.g., blue tit, *Parus caeruleus*, males and females; Hunt et al., 1999; zebra finch, *Taeniopygia guttata*, females; Bennett et al., 1996). In some cases, different studies offer conflicting results for the same species, but color does appear to be an important determinant of mating choices for both males and females in many bird species. For a more comprehensive overview of the role of color in mate choice in birds, see Hill (2006).

Interestingly, some birds use color not only on their bodies but also in constructed displays. For example, male bower birds construct large "bowers" to attract females. To do this, they collect colorful berries, feathers, and leaves and add them to their displays. These often seem to be chosen to maximize the chromatic contrast of the male bird against the bower (Endler and Day, 2006; Endler et al., 2005). Birds also seem to show sensory biases in their mate choice, exhibiting greater attraction to others when a particular color is present even when it is not a natural part of the body (Arak and Enquiest, 1993). Examples include finches that exhibit preferences for members of the opposite sex that have been given artificial leg rings (e.g., zebra finches, *Taeniopygia guttata*; Burley et al., 1982; Hunt et al., 1997; double-bar finches, *Poephila bichenovii*; Burley, 1986), and for individuals that have been given experimental crests (e.g., zebra finches, *T. guttata*, and long-failed finches, *Poephilia acuticauda*; Burley and Symanski, 1998), of particular colors. Biases towards preferences for such colors may be analogous to human situations where individuals wearing red clothing are considered more attractive (Elliot and Niesta, 2008; Guéguen, 2012; Roberts et al., 2010), and where black-and-white photographs of individuals of the opposite sex framed in red are rated by observers to be more attractive and sexually desirable (Elliot et al., 2010; Schwarz and Singer, 2012).

## Color and mate choice in non-human primates

In most primate species studied to date, color has primarily been linked to social status and dominance rather than mate choice *per se* (see Setchell, Chapter 26, in this volume). As high social status in primate males is often linked to high reproductive success, separating dominance and mate-choice effects can be difficult. Table 24.2 reviews the studies that have focused on assessing colors hypothesized to have an influence on color and mate choice in non-human primates, or have included measures of color with both mate choice and dominance status simultaneously. Several of these cases will be considered here in more detail.

One genus where color and mate choice have been studied quite extensively is *Mandrillus*. This genus consists of two extant species – the mandrill, which has been the focus of several color studies (e.g., Setchell and Dixson, 2001; Setchell and Wickings, 2005; Setchell *et al*., 2006, 2009), and the drill, the coloration of which was described by Hill (1955) and studied by Marty et al. (2009). These two species are closely related and parapatric, with their geographic ranges in west and central Africa divided by the Sanaga river in Cameroon. The mandrill is perhaps the most famous of all colorful primates, exhibiting a bright red nose surrounded by blue. Studies have linked the red colors expressed by mandrills to dominance, with high-ranking males exhibiting greater color expression than low-ranking males (Setchell and Dixson, 2001; Setchell and Wickings, 2005; Setchell, Chapter 26, in this volume). Changes in social status precede changes in coloration, with males obtaining alpha status subsequently increasing expression of red coloration, while males losing high social status experience a loss of coloration (Setchell and Dixson, 2001). This is a situation also found in gelada, where males taking over one-male units subsequently gain redder chest patches, while the chest patches of deposed males fade (Bergman

Table 24.2 *Studies assessing mate choice based on color in primate species*

| Species | Common name | Sex tested | Body region | Colors analyzed | Evidence for mate choice? | Preferences | References |
|---|---|---|---|---|---|---|---|
| *Eulemur fulvus* | Brown lemur | Female | Face | Image brightness | Yes | Brighter images | Cooper and Hosey, 2003 |
| *Hapalemur griseus occidentalis* | Bamboo lemur | Female | Face | Image brightness | No | No preference | Cooper and Hosey, 2003 |
| *Varecia variegata* | Red ruffed lemur | Female | Face | Image brightness | No | No preference | Cooper and Hosey, 2003 |
| *Macaca mulatta* | Rhesus macaque | Female | Face | Red | Yes | Increased redness | Waitt et al., 2003 |
| *Macaca mulatta* | Rhesus macaque | Male | Hindquarters | Red | Yes | Increased redness | Waitt et al., 2006 |
| *Macaca mulatta* | Rhesus macaque | Male | Face | Red | No | No preference | Waitt et al., 2006 |
| *Macaca mulatta* | Rhesus macaque | Male | Face | Red/green ratio, luminance | Yes | Ovulatory faces (highest red/green values and darkest luminance are displayed at peak fertility) | Higham et al., 2010, 2011; Dubuc et al., 2009 |
| *Macaca mulatta* | Rhesus macaque | Female | Face | Red/green ratio, luminance | Yes | Increased redness (high red/green values and low luminance values) | Dubuc et al., 2014a |
| *Mandrillus leucophaeus* | Drill | Female | Groin and lip areas | Multiple (principal-component analysis of RGB values) | No | No preference | Marty et al., 2009 |
| *Mandrillus sphinx* | Mandrill | Male | Sexual swelling | Red | No | No preference | Setchell et al., 2004 |
| *Mandrillus sphinx* | Mandrill | Female | Face | Red | Yes | Increased redness | Setchell, 2005 |
| *Papio ursinus* | Chacma baboon | Male | Sexual swelling | Red, orange, yellow, green, blue, purple | Yes | Red over all other colors | Bielert et al., 1989 |
| *Chlorocebus aethiops* | Vervet monkey | Female | Testicles | Blue | Mixed | Housed with males with dark testicles, preferred light testicles; housed with males with light or darkened testicles, no preference | Gerald et al., 2010 |
| *Pan troglodytes* | Chimpanzee | Male | Sexual swelling | Red | No | Increased redness | Breaux et al., 2012 |

et al., 2009). A recent study has emphasized the crucial role of the contrast between the red and blue coloration on the mandrill nose in dominance signaling – this chromatic contrast between red and blue is a better predictor of dominance status than either the red or the blue color alone (Renoult et al., 2011). Marty et al. (2009) showed that drill coloration is also related to dominance – males more saturated in red coloration were of higher dominance rank.

However, studies of the two species have come to different conclusions when it comes to female mate choice. Setchell (2005) used partial correlations to show that females exhibited more proceptive behaviors towards more colorful males when controlling for dominance rank (i.e., males who were more or less colorful than predicted from rank were more or less attractive than predicted from rank). In contrast, Marty et al. (2009) used similar methods to show that females did not prefer colorful males independently of dominance rank. Reproductive skew by male dominance rank is extreme in mandrills (Charpentier et al., 2005; Setchell *et al.*, 2005), and though reproductive skew in the drill is unknown, data on mating skew suggest that this is steep, and that mating is largely restricted to the top-ranked individuals (Marty *et al.*, 2009). Though statistical methods have been used to separate effects of dominance rank and coloration on female mate choice, the difficulty of separating male social status, male mating and reproductive success, and female preference for particular males in these species means that further studies are needed before we fully understand the potential role of coloration in female mate choice in this genus.

Another well-studied taxon is the mulatta macaque group, which consists of the rhesus macaque, Japanese macaque, and Taiwanese macaque (Groves, 2005). In rhesus macaques, studies have shown that male coloration is not related to dominance rank – higher ranked males are not more colorful (Dubuc et al., 2014a, 2014b;

Higham et al., 2013). Instead, coloration appears to be used in mate choice by both sexes. Males become redder and darker during the mating season, and females exhibit more proceptive behaviors towards darker-faced males (Dubuc et al., 2014a, 2014b). In addition, experimental manipulations of male faces have shown that females look longer at redder versions of male faces, also suggesting female preference for increased facial color expression in males (Dubuc et al., 2015; Waitt et al., 2003). Female faces get darker around the period of ovulation (Dubuc et al., 2009; Higham et al., 2010), and in choice tests males prefer to look at ovulatory over pre-ovulatory faces (Higham et al., 2011; but see Waitt et al., 2006). Although behavioral choice tests have not yet been published for Japanese macaques, tests of facial color variation alongside hormonal measurements have shown that females are more colorful around ovulation, indicating that this signal could also be used by males in mate choice in this species (Fujita et al., 2004). Collectively, we have the best evidence so far of the use of colors in primate mate-choice decisions for the closely related mulatta macaque group.

For many primate species living in multimale, multifemale social groups, where females have the opportunity to mate with multiple males (and potentially to choose between them), males fight over dominance (exhibit "direct" male–male competition). These species are often markedly sexually dimorphic – males are weaponized (e.g., relatively large canines and body size), and reproductive skew by male dominance rank is very steep, such that those individuals successful in obtaining alpha status obtain the majority of reproductive success. Under such circumstances, with males weaponized and much larger than females, and with high-ranking males dominating reproduction, there may be little scope for direct female mate choice, but strong selection on signals related to male–male social status signaling. Thus we suggest that the use of color in mate choice (intersexual) signaling, as opposed

to dominance (intrasexual) signaling, might be rare in non-human primates (Dubuc et al., 2014a, 2014b). However, where it occurs, it might be found more commonly in those species where males do not exhibit strong contest competition over dominance, and where female choice is a stronger mechanism by which male mating success is determined. This would include those macaque species with reduced reproductive skew, such as the mulatta macaque group, and human groups, which in many societies exhibit social monogamy within wider fission–fusion multimale, multifemale societies.

## What is being "chosen"?

Although individuals may be more attractive on the basis of bright colors, this may often be a proxy for other desirable characteristics. Colors may be related to underlying qualities of individuals, with increased expression of particular colors attractive to members of the opposite sex because selection is acting to favor males or females that select for the underlying trait (rather than the color *per se*). For example, colorful birds may be advertising their high carotenoid levels, and hence their fitness and ability to collect these pigments from the environment (Hill and Montgomerie, 1994; Senar and Escobar, 2002). In both human and non-human primates, red skin coloration is linked to the flow of oxygenated blood, so that color changes may signal underlying health. These traits may in turn reflect underlying beneficial genetic properties related to health and durability that are preferred in mate choice, because the offspring resulting from the mating will also possess these properties. This is known as mate choice for "indirect benefits," with the indirect benefits under selection usually related to "good genes." This contrasts with mate choice for "direct benefits," where the choosing individual gains tangible benefits such as the provision of a nest, territory, or food. The ability to provide such direct benefits may also be signaled

through coloration. For example, high-ranking primate males that advertise their dominance through coloration might theoretically be attractive to females because of their ability to provide protection from predators and conspecifics, and preferential access to food sites. Similarly, in addition to or instead of signaling good genes by exhibiting colorful carotenoids in their tissues, birds may be advertising their ability to collect resources from the environment and hence to provision for young (to provide direct benefits).

There are, however, other explanations for the evolution of preferences for particular color signals that are less adaptive. Species may develop sensory biases in one context, such as preference for ripe, red fruit (Fernandez and Morris, 2007). A preference for red evolved in a feeding context may lead to a general preference for red coloration, which can manifest itself in greater attraction to red individuals. Such biases are open to exploitation by signalers, who over evolutionary time may increase their signal expression to further enhance their attractiveness to conspecifics (sensory exploitation) (Endler, 1992; Ryan, 1990). Once a preference for a particular trait has evolved, continued preference for the trait and further exaggeration of the trait can also co-evolve in a separate process called Fisherian ("runaway") selection. Under this process, expression of the trait and preference for the trait are genetically linked, such that individuals inherit both the trait (which may only be expressed in one sex) and the preference for the trait (which may only be expressed in the other). Models show that this process feeds back on itself over evolutionary time, leading to ever stronger trait expression and preference for ever stronger trait expression, until the signal is opposed by another process (Fisher, 1930; Lande, 1981).

## Form and function

While human and non-human primates are known for their use of red coloration in mate

choice, red colors are far from the only colors utilized by non-humans, and even closely related species may exhibit very different color types. For example, birds of paradise exhibit many different colors in their displays, and these vary between species. Despite the differences in the particular colors males of each species use, all species appear to be using them to attract females (i.e., they are being used for the same function). As such, understanding the function of colors (e.g., social status versus mate choice) is not fully informative about which colors might be utilized to fulfill the function (e.g., blue versus red versus yellow). There are several factors by which the form of colors is influenced (e.g., production mechanisms, visual systems, the environment; see above), and it would be unfair to say that no studies have considered the perceptual and ecological mechanisms that give rise to color form. Theoretical and related mechanisms of sensory drive, sensory biases, sensory exploitation, and so on, and their effects on signal form and signal efficacy, have been much considered by animal-communication researchers (e.g., Arak and Enquiest, 1993; Dawkins and Guilford, 1996; Endler and Basolo, 1998). Nonetheless, more studies need to focus on elucidating the links between form and function, and ask questions not just about what colors do in a given species but also why those particular colors do it.

## Current and future directions

Here, we briefly consider some of the directions in which investigations into color and mate choice are heading. Some of these, but not all, apply to animal coloration more generally.

Increasingly, researchers are integrating measures of color with measures of visual systems. This can be done with knowledge of the number of retinal receptor types in different species, as well as their spectral sensitivities. Typically, colors can be plotted in color spaces based on the visual system of each species. For example,

Stoddard and Prum (2008) plotted the colors of New World buntings in a tetrahedral space in which each point of the tetrahedron represents an avian photoreceptor, and where the position of each color inside the tetrahedron represents the relative stimulation of each photoreceptor in response to the color. Beyond such quantal catch mapping, it is also possible to estimate the likely discriminability of different colors (i.e., the degree of detection error around one color and whether that error is likely to overlap between two colors – just noticeable differences (JNDs)), using models such as the receptor noise model (Vorobyev and Osorio, 1998). For example, Higham et al. (2010) plotted variation in the facial color and luminance of rhesus macaques, using this model, to show how variation in facial luminance across the female fertile phase is perceptible to male rhesus macaques who are choosing which female to mate with. One advantage of such discrimination models is that one can create stimuli that are carefully calibrated to receiver perception for experiments. Higham et al. (2011) used images of fertile and non-fertile female rhesus macaques to test male responses. In doing so, they reproduced female colors indiscriminably different from those originally displayed by the males. Further, it is possible to create color manipulations in which the color created and presented varies in specific units of discriminability to that species (JNDs).

In addition to analyzing and recreating colors in perceptually relevant units, studies are beginning to measure color patterns in ways that are representative of how such patterns are perceived within the brain. Allen et al. (2014) have taken a computational "eigenface" approach to looking at non-human primate faces, focusing on guenon monkeys. The eigenface approach extracts the principal axes of variation in complex visual patterns in a way thought to be similar to how such patterns are encoded by the primate brain (Rhodes and Jeffery, 2006). Similarly, Allen and Higham (2015) segmented specific traits from

guenon faces, such as colorful nose spots and eyebrow patches, using a pulse-coupled neural network (PCNN; Johnson, 1994), specifically the NSCT-SF-PCNN (Qu et al., 2008). In this model, each pixel corresponds to a neuron that receives inputs from neighboring neurons. When the sum of inputs exceeds a threshold, the neuron gives a pulse output to neighboring neurons, equivalent to an action potential in the primate primary visual cortex. Outputs become synchronized, so that over a number of iterations the series of pulse outputs defines the regions in an image by forming autowaves. The process results in a map of neuron firing times based on simplified mammalian early vision, and patch regions are then selected from this map. Methods of visual scene assessment and pattern recognition such as this, which are based on appropriate perceptual processing rather than any other type of measurement, may be more likely than other methods to produce relevant measures of color patterns and shapes that represent how animals see the world.

Another area that seems ripe for use in the assessment of animal mate-choice signals is the use of machine classifiers. Algorithms can be used to assess the variation in facial color patterns – for example, to determine whether differences in species can be reliably determined by facial color patterns (Allen et al., 2014), and whether male facial color patterns are reliably different from those of females (Allen and Higham, 2015). In addition to machine classifiers, a highly complementary approach is the use of the "looking-time" paradigm to investigate mate-choice signals in experiments with live animal receivers. To do this, images are often presented side by side, and subject responses are recorded by video cameras to determine which image attracts longer looking times. This longer looking time is used as a proxy of interest or attraction to that particular stimulus. This is based on work in experimental psychology on preverbal infants (Fantz, 1963), and has been validated for use in non-human primates by several approaches, including experiments showing that rhesus monkeys look longer at images of rhesus monkey faces than at controls (Deaner et al., 2005), and look longer at images of their own species than those of others (Demaria and Thierry, 1988; Fujita, 1987). In studies of rhesus macaque mate choice, this technique has been used to show that females prefer artificially reddened faces of males (Waitt et al., 2003), that males familiar with females choose ovulatory over pre-ovulatory faces (Higham et al., 2011), and that rhesus macaques are more attracted to black-and-white images of conspecifics when placed in red rather than blue frames (Hughes et al., 2015), in a manner similar to humans (see above). A widening of this approach to investigate mate choice in more species and with more traits could be fruitful, as long as potential methodological limitations and caveats are carefully considered (Winters et al., 2015).

One final direction that we would like to highlight is the assessment of color heritability. Showing that colors are used in mate choice is an important step, but understanding coloration more fully as a sexually selected trait requires demonstration of the heritability of the trait, and, ideally, of the strength of selection acting on it (the selection gradient). This requires a great deal of data – measures of color for mothers, fathers, and adult offspring; genotypic paternity data for heritability; and data on the reproductive success of individuals of different color expression for the investigation of selection. Analyses of heritability and/or the strength of sexual selection in color signals are underway, utilizing large data sets for primate species including rhesus macaques (Dubuc et al., 2014b) and mandrills (Setchell *et al*., 2014).

## Conclusion

There is a great deal of evidence for the use of color in mate choice in non-humans, but this

is taxon specific. In taxa where intersexual selection and female mate choice are strong mechanisms, such as birds and fish, there is much evidence for the role for coloration in mate choice through ornaments that are attractive to the opposite sex. Among mammals, where intrasexual selection and male–male competition are primary mechanisms by which males compete for females through fighting, color ornaments involved in mate attraction are rare. An exception is the non-human primates. However, even here many species compete for females primarily through competition over dominance and social status. Exceptions include those species where differences in social and mating systems have led to decreased direct competition over dominance. Primary examples include those macaque species with reduced reproductive skew, such as rhesus macaques and Japanese macaques, and humans, who exhibit social monogamy. Both circumstances are associated with reduced sexual dimorphism and hence increased scope for direct female mate choice. Increased direct female mate choice among such species increases the level of selection for ornaments rather than weapons, and makes the evolution of a role for color in mate choice more likely.

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