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## Evolution of female coloration: What have we learned from birds in general and blue tits in particular

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**Running title:** The **evolution** of female coloration in birds

**Title: Evolution of female coloration: what have we learned from birds in general and blue tits in particular**

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- **Abstract of 250 words**

Female ornaments have long been considered non-functional, but a paradigm shift has occurred over the two last decades. The adaptive nature of female ornaments is now widely accepted. After a rapid overview of this shift, we present the results of comparative studies focused on identifying the forces involved in the evolution of female coloration in birds. We then discuss the results of intraspecific **ornithological** field studies and finish up by **summarising** the work done by our group and others on female coloration in blue tits (*Cyanistes caeruleus*). Overall, this review confirms that female coloration traits function as ornaments and/or badges of status in many bird species. It also identifies several mechanisms that can circumvent trade-offs in investment between coloration traits and egg production. Based on this review, we call for further research on certain topics and specific changes in practices. More precisely, at the macroevolutionary level, we should avoid framing our questions around sexual dichromatism and male-centered proxies of sexual selection if we wish to elucidate the female-specific selective forces and constraints involved in the evolution of female coloration. At the microevolutionary level, we need to quantify social and sexual selection in both sexes, and to perform experimental studies to compare the selective forces acting on female and male coloration. In particular, it appears important to investigate how maternal effects and physiological drivers of aggressiveness relate to female coloration. Finally, our work on blue tits illustrates the importance of conducting long-term studies in tandem **with replicated experiments** within a given species.

## 1- Introduction—female ornaments: a paradigm shift

Animal **armaments and ornaments** are exaggerated signals that increase **respectively** access **to resources through dominance** and mating success. They evolve through intersexual selection (i.e., mate choice Fischer, 1930), and/or social selection (Lyon & Montgomerie, 2012; West-Eberhard, 1983). **Because they are often more extreme in males, these traits are predominantly portrayed as male traits**, leading to an asymmetrical perspective, which views sexual and social forces as placing greater selective pressure on male traits. **Proposed explanations for it can be traced back to the work of Bateman and Trivers** (Bateman, 1948; Trivers, 1972 (Bateman, 1948; Trivers, 1972)).

Several landmark studies provide an explanation for why sexual traits are often viewed as less likely to evolve in females. First, in an experiment on *Drosophila*, Bateman found that male reproductive success was much more variable than female reproductive success. He also found a positive relationship between mate number and reproductive success (i.e., number of offspring sired) in males but not in females. He proposed that this result could be partly explained by anisogamy. While males produce a large number of small, inexpensive gametes, females produce a comparatively smaller number of large, costly gametes, resulting in a different initial investment in individual offspring. Although this Bateman principle is **debatable** (Gowaty, Kim, & Anderson, 2012; Tang-Martínez, 2016), a recent meta-analysis found support for Bateman's hypotheses and indicated that, in many animal species, the relationship between mate number and reproductive success is more common in males than in females (Janicke, Häderer, Lajeunesse, & Anthes, 2016). Second, Trivers (1972) showed that interspecific differences in parental care could explain conventional sex roles (i.e., sex-specific behavior during mate acquisition and/or parental involvement, parental care being defined as a costly parental investment that increased offspring survival). He showed that any sex-based

differences in parental care should lead the sex that invests the most in offspring—generally females—to become a limited resource for which the other sex competes. Mate choice should therefore most benefit the sex with the greatest investment in offspring if this enhances offspring survival, thus inducing a positive feedback loop (Henshaw, Fromhage, & Jones, 2019). Last, several authors argued that a male bias in the operational sex ratio (i.e., the ratio of males and females available for reproduction in the population) could also explain weaker sexual selection on female traits because if females face less competition for mates then male mate choice should be more relaxed (Edward & Chapman, 2011). Given this background, it is clear why conspicuous traits in females have long been considered as no more than anecdotal.

In addition, alongside anisogamy, the cost of reproduction has frequently been cited to explain why ornaments and armaments have not evolved in females. This argument is based on the assumption that females are more sensitive than males to the possible signaling costs and posits that cost can manifest itself in two ways. First, the cost of producing certain exaggerated traits could be prohibitive if it affects a female's ability to invest in offspring and there is no compensating investment by males. In such a case, allocating large amounts of resources to ornament production could negatively affect egg quality and fecundity in females, leading to a trade-off (Fitzpatrick, Berglund, & Rosenqvist, 1995). Second, the cost could be associated with ornament display. More specifically, Wallace predicted that females that invest more in reproduction (e.g., by incubating their eggs) than males face greater predation risks, favoring selection for more cryptic females (Wallace, 1877). Support for Wallace's hypothesis has been found in comparative studies showing that females tend to be more cryptic in species with more visible nests (Martin & Badyaev, 1996; Soler & Moreno, 2012). Finally, males may harass highly attractive females, decreasing their fecundity and latter's survival and thus intensifying selection against more ornamented females (Hosken, Alonzo, & Wedell, 2016).

However, several reasons have led to question the classical [asymmetrical](#) view exposed above [and to question the origin and evolution of female ornaments](#). First, the biological reality is that there are many species where both females and males are conspicuously ornamented. Even in sexually dimorphic species, females are rarely completely drab, and many females bear at least one conspicuous trait. For example, in various duck species with strong sexual dimorphism, females display conspicuous wing bars. Also, research on reproductive roles revealed that differences in sex-specific investment can shift rapidly if ecological conditions change. [For instance, in the two-spotted goby fish \*Gobiusculus flavescens\*”, sexual selection is varying within the breeding season. This temporal variation is due to a complete reversal of sex roles across the breeding season, driven by a change in the operational sex ratio heavily male-biased at the start of the season then heavily female-biased towards the end of the season\(Amundsen, 2018\)](#). Last, the assumption that all ornaments need to be costly or [are subjected to allocation trade-offs](#) is the subject of debate (Prum, 2010; Weaver, Koch, & Hill, 2017). Consequently, understanding why female ornaments exist and how they vary among species is a topic that clearly merits interest.

Several results concur to lead for a call for a paradigm shift (Amundsen, 2000). Among the first voices were Jones and Hunter, who conducted one of the earliest experiments to find evidence of male preference for female ornaments in a monogamous bird species, the crested auklet, *Aethia cristatella* (I. L. Jones & Hunter, 1993). Roulin *et al.* also produced several papers showing that female ornaments had a function in the barn owl, *Tyto alba* (Roulin, 1999; Roulin, Jungi, Pfister, & Dijkstra, 2000; Roulin, Riols, Dijkstra, & Ducrest, 2001). A landmark study on the eclectus parrot (*Eclectus roratus*) suggested that red coloration in females resulted from fierce female-female competition (Heinsohn, Legge, & Endler, 2005). Around this same period, several comparative studies revealed that female ornaments had evolved independently on numerous occasions: they found that gains and losses of ornamentation often occurred

separately in males and females, and that female traits seemed to be more labile than male traits (Burns, 1998; Irwin, 1994; Ord & Stuart-Fox, 2006; Wiens, 1999).

Although the paradigm for understanding the evolution of ornaments then shifted, the more classical, asymmetric perspective was still favored to understand the evolution of female ornaments. The lability of female ornaments was mainly thought to be the result of genetic correlations with male ornaments (Lande, 1980) tempered by the strength of natural selection (Wallace, 1877) or driven by more balanced sex roles (Trivers, 1972). This genetic correlation hypothesis treats the evolution of female ornaments as a non-adaptive byproduct of sexual selection on male traits that is consequently shaped by the limited genetic variation available for sex-dependent expression (Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007; Price, 1996). A classical study supporting this hypothesis involved a cross-fostering experiment in zebra finches (*Taeniopygia guttata*): red bill coloration was explained by a strong genetic correlation between fathers and daughters (Price, 1996). However, species displaying conventional sex roles highlight a major mathematical issue with this idea: if conspicuous female traits were solely byproducts, there should be no variation in sex-dependent trait expression; in other words, the genetic correlation between the sexes should be exactly 1 (Lande, 1980), a relatively unlikely situation. Moreover, models have shown that male sexual traits that are pleiotropically expressed in females can only evolve if females express a very attenuated form of the trait (Servedio & Lande, 2006). Finally, recent work suggests that ornament expression can easily be labile if ornaments arise later in development (Kraaijeveld, 2014). Therefore, although genetic correlation clearly played a key role in the evolution of the female ornaments, it cannot fully explain the equally intense expression of traits by both females and males in many species. It follows that female traits may be adaptive as a result of predation pressures but may also be under other selective forces. More specifically, female traits could function as (i) signals for attracting males and/or (ii) signals used during sexual or social competition among females.

(i) Male mate choice—In the late 1990', theoretical research identified **some** conditions under which the evolution of mutual mate choice should be favored (Johnstone, Reynolds, & Deutsch, 1996; Kokko & Johnstone, 2002). These models **suggested** that male mate choice evolves when there is variation in female quality and there are limits on male reproductive potential, which **means that under these conditions, choosier males will more likely increase their reproductive success than indiscriminating males**. Variation in female quality, on one side, is seen in a wide variety of taxa **across the animal kingdom**. For instance, in several species, female size is positively correlated with fecundity, and males seem to prefer larger females (Nordeide, Kekäläinen, Janhunen, & Kortet, 2013). Coloration patterns are also variable and sometimes linked to female reproductive potential: for instance, in two-spotted gobies (*Gobiusculus flavescens*), yellow-orange belly coloration is correlated with fecundity in females, and mate choice experiments have revealed that males prefer females with more brightly colored bellies (Amundsen & Forsgren, 2001). On the other side, male reproductive potential is limited by (i) the risk associated with rejecting a potential mate (which depends on encounter rate) (Barry & Kokko, 2010) and (ii) time and energy budgets. Time spent competing for and/or attracting a mate as well as the time spent providing parental care reduces the time available for mating with other individuals and thus decreases an organism's total number of mates. Energy budgets are influenced by the cost of sperm production and quality, which may be particularly important in polygynous species in which there is no paternal care and males have relatively unlimited access to females (Reinhold, Kurtz, & Engqvist, 2002). Sperm limitation is the main argument used to explain why, in polygynous feral red junglefowl (*Gallus gallus*) and stalk-eyed flies (*Teleopsis dalmanni*), males transfer more sperm to females with larger combs (Cornwallis & Birkhead, 2007; Pizzari, Cornwallis, Lovlie, Jakobsson, & Birkhead, 2003) and larger eyespan (Cotton, Cotton, Small, & Pomiankowski, 2014), respectively. Consequently, abundant theoretical and empirical evidence favor the view that male mate choice **is more widespread**



than previously thought in monogamous or polygynous species displaying conventional sex roles (Hare & Simmons, 2019; Kraaijeveld, et al., 2007; Schlupp, 2018).

(ii) Female-female competition—The hypothesis that conspicuous female traits evolved as armaments signaling fighting ability, otherwise known as “badges of status,” started to garner attention in the mid-2000s (Clutton-Brock, 2007, 2009; Clutton-Brock et al., 2006; Lebas, 2006), even if it was suggested much earlier (West-Eberhard, 1983). The competitive functions of female ornaments have been illustrated by work in a number of taxa (Clutton-Brock & Huchard, 2013; Rosvall, 2011; Rubenstein, 2012; Stockley & Bro-Jørgensen, 2011; Tobias, Montgomerie, & Lyon, 2012). At present, many researchers consider that social selection (i.e., competition for food, dominance, and territories) has played a major part in the evolution of female ornaments. Indeed, female-female competition may generate dramatic differences in fecundity and reproductive success among individuals, beyond what would be expected based on intrinsic female quality only. Also, the resources gained, which can be invested in future fecundity, could outweigh signaling costs. Finally, it is currently hypothesized that competitive context differs for the two sexes: female traits might more often evolve to mediate competition for ecological resources, while male traits might more often evolve to mediate competition for mate acquisition and resources (Stockley & Bro-Jørgensen, 2011; Tobias, et al., 2012).

So overall there are now many studies suggesting that female conspicuous traits should also evolve through sexual or social selection and may even sometimes fulfil dual functions (i.e. be sexual ornaments and badges of status, e.g., Berglund & Rosenqvist, 2009).

## 2. Aim of this review

The overview above shows that the paradigm for understanding the evolution of ornaments has gradually shifted over the years and that it is now widely accepted that female ornaments may have an adaptive function. It is now also considered that differences in traits between the

sexes may be qualitative, quantitative, or nonexistent. Given that several reviews have already been written on this subject (see the references above), our goal here is to focus on what is known about the evolution of female ornaments in a specific class of animal—birds, with the aim of better identifying ideas that remain overlooked or that are weakly supported. [In addition we also](#) discuss current gaps in knowledge and propose better methods for testing hypotheses. The byproduct hypothesis will not be addressed in detail as it was explored in a review on the genetic architecture of female ornaments (Kraaijeveld, 2014). However, it is obviously one key driver of female—and male—ornamentation (Amundsen, 2000).

Birds represent interesting models for exploring the evolution of female ornaments because variation in their life-history traits can be used to study the complex interplay between evolutionary forces and constraints. For instance, theoretical models have identified biparental care and life-long social monogamy as factors that favor the evolution of male mate choice (Johnstone, et al., 1996; Kokko & Johnstone, 2002). These characteristics are both common and highly variable across bird species (Cockburn, 2006). Furthermore, variability in sociality over the winter, male parental care, territory quality, and sperm quality can be used to study the function of female ornaments in the context of female-female competition.

Birds employ two main forms of communication: acoustic and visual communication. In most textbooks, song is presented as a male-specific signal. However, very recently, female bird song was found to occur in 64% of extant songbird species (Odom, Hall, Riebel, Omland, & Langmore, 2014), illustrating the strength of bias in perspectives on research. Because several reviews have recently been published on female acoustic communication (Amy, Salvin, & Leboucher, 2018; Riebel, Odom, Langmore, & Hall, 2019), we will focus here on female visual communication, namely coloration (see Box 1 for more details). While we will mostly review work on female plumage, we will also deal somewhat with female bare-part ornaments. Also,

although we discuss female eggshell coloration in passing, we will not extensively review that vast subject (Moreno & Osorno, 2003).

In the first part of this review, we assess advances in our understanding of the forces shaping female coloration in birds by evaluating the results of recent comparative studies. Because most of these comparative studies were conducted to understand the evolution of dichromatism, the conclusion is that there remains an acute need to examine the sex specific selective forces underlying evolution of female coloration in birds. Then, we look at long-term studies in relation to what they have revealed and could reveal about the influence of sexual and social selection on female coloration traits in birds, and we present what is currently known about the signaling content of female coloration. This focus paves the way to discuss (i) whether ornament cost impedes the evolution of female coloration in birds and (ii) to evaluate the benefits choosy males might obtain beyond simply mating with partners that are more fecund. (iii) It also leads to assess the results of experimental and physiological studies that tested whether female coloration traits could serve as badges of status. The conclusions of this second & third parts of the review are that long-term studies are needed and that future research should focus specifically on the relationship between maternal effects and female coloration in birds; dig deeper into the physiological basis of female coloration and aggressiveness; and test the importance of inter and intrasexual selection on ornaments in both sexes simultaneously. In the third part of the review, we describe research focused on one single bird species, the blue tit (*Cyanistes caeruleus*), a [well-studied](#) biological model for which we have gathered data on coloration and life-history traits in different study populations over many years. We thoroughly examine the work done by our group and other groups throughout Europe. The conclusions for this third part of the review are that studying different populations of the same model species can help critically assess the generality of observed patterns and [point limitations and dangers of using too low sample size](#). Research on a single model also show that it is important to

independently replicate studies using the same or complementary methods; and to run long-term studies to determine the forces behind the evolution of female ornamentation.

### 3. Macroevolution of female coloration—insights from comparative studies

Historically, comparative studies provided indirect insights into the evolution of female coloration while trying to understand the evolution of sexual dichromatism. Essentially, sexual dichromatism was thought to have arisen from intense sexual selection acting on males. As expected, several studies found that polygynous species were more likely to be sexually dichromatic and that socially monogamous species were more likely to be sexually monochromatic (Bennet & Owens, 2002; but see Dunn, Whittingham, & Pitcher, 2001; Price & Eaton, 2014). Some also found that levels of extrapair paternity (i.e., genetic mating patterns (Møller & Birkhead, 1994) appeared to be tied to dichromatism. Yet other factors, either unrelated or only indirectly related to sexual selection in males, were also found to be associated with sexual dichromatism; they included latitude, paternal care, and parasitism (Scott & Clutton-Brock, 1990) but also nest ecology (Martin & Badyaev, 1996). Meanwhile, studies in Icteridae (Irwin, 1994) and Thraupidae (Burns, 1998) revealed that [variation in sexual dichromatism was better explained by variation in female rather than male coloration](#). Based on these studies, calls began for research to include variation in both female and male plumage to better understand the evolution of sexual dichromatism, and avoid using sexual dichromatism as a proxy for the intensity of sexual selection (see Box 2 for more details and Figure 1).

However, [most recent](#) comparative studies still adopted a biased perspective and worked within the [framework](#) of sexual dichromatism. More specifically, they tested potential limitations placed on the evolution of female coloration by ecological factors such as migration (Friedman, Hofmann, Kondo, & Omland, 2009), nest characteristics, and habitat openness (Soler & Moreno, 2012). The first comparative study to explore evolutionary forces that might

accentuate female coloration was not published until 2009. Still framing their questions from the perspective of sexual dichromatism, Rubenstein and Lovette tested how cooperative breeding could reduce the degree of sexual dimorphism by favoring the occurrence of conspicuous plumage in female African starlings (Sturnidae). Cooperative breeding is a mating system in which sexually mature individuals help raising the offspring of others (Cockburn, 1998), meaning that only a few individuals have access to reproduction, which results in intense competition for mating in both sexes and favors monochromatism. In this study, cooperative breeding species were more likely to be sexually monochromatic than were non-cooperative ones, underscoring that competition may be an important factor in the evolution of female coloration (Rubenstein & Lovette, 2009). Yet, more than a decade after studies showing that female coloration could be labile (Irwin, 1994), comparative research still had not stepped outside the sexual dichromatism framework when examining evolution of female plumage coloration.

In 2015, two studies addressed the evolution of female plumage coloration together with male coloration and dichromatism (Dale, Dey, Delhey, Kempenaers, & Valcu, 2015; Dunn, Armenta, & Whittingham, 2015). Although the studies differed in their methods for assessing plumage coloration (i.e., color estimated from book plates vs. spectrophotometry), they used a similar statistical approach: after testing how well certain indices predicted variability in both female and male coloration (i.e., within the framework of sexual dichromatism), they then looked at coloration in each sex separately (aiming at breaking down the composite nature of sexual dichromatism). Both studies found that most of the variation in plumage dichromatism was explained by factors acting on female coloration, not male coloration. Dale et al. (2015) found that indices associated with living in the tropics (i.e., lower latitude, yearlong nesting, smaller clutch size) or higher body mass tended to enhance the likelihood of female coloration, while migration tended to limit it (Dale, et al., 2015). Interestingly, while this study found that indices

of intense male sexual selection (social polygyny, lack of paternal care) were positively correlated with sexual dichromatism, this relationship largely arose from a negative correlation with female coloration rather than from a positive correlation with male coloration. Additionally, the method used by Dale and colleagues made it possible to suggest that the genetic correlation between female and male coloration is strong. Dunn et al. (2015) found that presence of sexual monochromatism was associated with indices of natural selection (i.e., migratory behavior, breeding in the tropics, paternal care, nesting ecology, body mass), while sexual dichromatism was associated with indices of both sexual selection in males (i.e., social mating system, ratio of testes size to body mass) and natural selection (nest height, paternal care) (Dunn, et al., 2015). This study also confirmed that sexual dichromatism was more related to evolutionary changes in females than in males.

However, from the perspective of this review, these two important studies (Dale, et al., 2015; Dunn, et al., 2015) shared a significant limitation: they used proxies traditionally associated with sexual selection in males, which are poorly suited to examining the influence of female-biased sexual selection. For instance, social mating system type—essentially monogamy or polygyny—mainly reflects the intensity of sexual selection in males. The presence/absence of paternal care also serves as a proxy for sexual selection in males, as well as for natural selection in females. This two-faceted nature of the latter variable may explain why, in contrast to Dale and colleagues, Dunn and colleagues treated presence/absence of paternal care as an ecological factor rather than as a proxy of sexual selection. Consequently, neither social mating system type nor the presence/absence of paternal care may be helpful indices if the goal is to understand how sexual selection in females shapes female coloration. It would be better to stop treating paternal care as a binary variable and to instead examine variation in male investment across different stages of parental care; the latter may better reflect dynamics of sexual selection in females, since males that invest more may be choosier about their mates (Johnstone 1996,

Kokko 2002), while females may compete for males that provide a greater degree of care. In line with this proposition, Soler and colleagues found that, in larger species, females were more conspicuous (i.e., displayed conspicuous monochromatism) when males participated in nest building (Soler, Morales, Cuervo, & Moreno, 2019).

The focus on sexual dichromatism instead of on sex-specific coloration has led to overlook the importance of patch location and size in the evolution of female coloration- females may use different body parts than males for signaling and may use smaller patches to remain more cryptic if they are more vulnerable to predation, for instance during incubation. Historically, comparative studies tested whether sexual selection was acting on body parts associated with visual communication in males—the crown, nape, throat, and breast—and, indeed, they found that these parts were more often dichromatic and/or conspicuous (Delhey, 2019; Gomez & They, 2004, 2007). However, visual communication in females might involve smaller and/or more concealed patches due to the antagonist pressures of natural selection. A handful of recent comparative studies on sexual dichromatism have looked at the location of color patches thought to serve as visual signals. They revealed that sexual dichromatism in patch coloration is explained by male-biased sexual selection in Thraupidae (Shultz & Burns, 2017) and Tyranninae (Cooney et al., 2019) and by female-biased natural selection in Maluridae (Medina et al., 2017); in the latter case, exposed female traits were more cryptically colored in open habitats than in closed habitats. Schultz and Burns (2017) also found that evolutionary changes in female coloration were reflected in wing primary feathers and tail feathers and were constrained by natural selection. Thus to better understand the evolution of female coloration, future studies should focus on characterizing the size and location of female-specific color patches and then examine how they are influenced by indices of sexual, social, and natural selection specific to females.

Finally, focusing on the coloration types displayed by birds should yield insights into whether costs might prevent the evolution of female coloration in species where females invest more in parental care than males. The costs associated with signaling may be related to the mortality risks associated with conspicuousness and more conspicuous colors may be avoided more frequently in females than males. Also, physiological costs might cause some colors to occur less frequently in females than males. For instance, carotenoid-based colors (i.e., yellow, orange, red) are sometime hypothesized to be more costly than melanin-based colors (e.g., black, gray, brown, rusty, orange-red: Galván & Wakamatsu, 2016) or psittacofulvin-based colors. This is because carotenoids are photosynthetic pigments that birds must obtain from dietary sources and because their incorporation into signals means that they are no longer available for other physiological processes, such as detoxification and immune function (Hasselquist & Nilsson, 2012; but see for a contrasting perspective: Koch & Hill, 2018; for review see: Olson & Owens, 1998; for a meta-analysis see: Simons, Cohen, & Verhulst, 2012; Svensson & Wong, 2011). Furthermore, carotenoid processing is affected by certain essential cellular features, such as vitamin A metabolism and redox state (Hill & Johnson, 2012). The situation is similar for structural coloration that is also sometimes expected to be less costly to produce than carotenoid-based colors (Prum, 2006). Structural coloration presents a broader diversity of colors than pigmentary colors (Delhey, 2015; Stoddard & Prum, 2011) and is produced by the physical interaction between light and feather microstructure ( Prum, 2006). Potential differences in costs (linked to physiology or conspicuousness) for the different types of colorations may explain why the color gamut available for females is less extended than for males (Delhey, 2015). Too high contrast (which may decrease crypsis) has also been put forward to explain why females of Western Palearctic species use more pheomelanin (which is lighter brown) than eumelanin in their signals (Negro, Figueroa-Luque, & Galván, 2018). Based on the assumption that coloration types have different costs, researchers have also hypothesized



that carotenoid-based colors should be more widespread than other types of colors in sexually dichromatic species. Species utilizing carotenoid-based colors have been found to be more sexually dichromatic in certain groups: North American passerines (Gray, 1996), Cardueline finches (Badyaev & Hill, 2000), Australian passerines (Delhey & Peters, 2017), and pigeons (Mahler, Araujo, & Tubaro, 2003; Taysom, Stuart-Fox, & Cardoso, 2011). Also, in males of the Tyrannidae family, carotenoid-based colors evolved faster in dichromatic species and within body regions commonly involved in intersexual or intrasexual displays (e.g., the crown, throat, breast, and/or rump). In females, however, no such pattern has been seen (Cooney, et al., 2019). We need more studies, which think beyond sexual dichromatism and investigate each sex separately. Characterizing the gamut of colors in females and exploring how it is influenced by female-biased sexual selection or social selection is thus another necessary step in the quest to identify the main evolutionary forces underlying female coloration.

**Summary** -To conclude this section, it is evident that several changes must be made if we wish to clarify the relative importance of the different factors shaping female coloration. First, we are still sorely lacking research that focuses on the evolution of female coloration. Second, studies looking at social and sexual selection in females should use appropriate proxies of these selection pressures (e.g. [densities](#), [skewed sex ratio](#), [paternal investment](#), [maternal investment](#)). The use of those that reflect sexual selection in males (e.g. [polygyny](#), [testes size](#), [absence of paternal care](#)) should be avoided [if looking at the effect of social and sexual selection in females](#). Last, one difficult aspect we faced in this review was the lack of [methodological consistency between studies](#), especially in assessments of coloration. Methods ranged from using the human eye to discretely score coloration to using photographs that were assessed from the perspective of avian visual space to defining principal components from spectrophotometric data (Table 1). Obviously, these differences made it difficult to properly interpret and compare the results. We

strongly encourage future studies to use more precise methods for quantifying coloration traits (see the details in Box 1 and 2).

(Table 1 about here.)

#### 4. Microevolution—insights from long-term studies

When Darwin proposed his theory of evolution (Darwin, 1859), he defined three conditions that are needed for evolution to occur under selection: (i) variation in the focal trait, (ii) inheritance of trait value, and (iii) a relationship between the trait and fitness. In other words, when the value of an inherited trait allows an individual to reproduce more successfully, evolutionary changes follow.

(i) **Variability:** female coloration displays a notable level of phenotypic variation. For instance, a study conducted on six passerine birds, the Eurasian blackcap (*Sylvia atricapilla*), the European robin (*Erithacus rubecula*), the blue tit, the great tit (*Parus major*), the common blackbird (*Turdus merula*), and the European greenfinch (*Carduelis chloris*), found that female coloration varied as much as male coloration in both sexually monochromatic and dichromatic species (Delhey & Peters, 2008).

(ii) **Heritability.** The heritability of coloration traits in birds has still rarely been quantified but so far, most components of coloration appear to be heritable and more and more studies manage to identify the genetic basis of switches in pigment types, colour intensity and colour pattern (e.g. Lopes et al., 2016; Mundy, 2018; Poelstra, Vijay, Hoepfner, & Wolf, 2015; Roulin & Ducrest, 2013). Studies have found that the heritability of color patch size is high (ranging from 0.28 to 0.90 for melanin and white patches, i.e.: Hubbard, Jenkins, & Safran, 2015; Roulin & Jensen, 2015; Saino et al., 2013). Melanin is endogenously synthesized in specialized cells (melanocytes), and its production is thus strongly genetically determined, which can explain the high heritability of melanin-based coloration (Ekblom, Farrell, Lank, & Burke, 2012;

Mundy, 2005). **Studies found** indices of color intensity and brightness **of chromatic colorations (yellow, blue)** to be heritable, even to a lesser extent (Charmantier, Wolak, Grégoire, Fargevieille, & Doutrelant, 2017; Evans & Sheldon, 2011; Hadfield et al., 2006; but see: Vergara, Fargallo, & Martínez-Padilla, 2015). **Sex-specific estimates of heritability have rarely** been computed. In blue tits, the chromatic component of structural coloration is heritable in both sexes, and the heritability of carotenoid chromaticity tends to be higher in males than in females (Charmantier, et al., 2017). Sex-specific heritability values can be calculated by assuming autosomal inheritance, as was done for blue tits in the study mentioned above, or by assuming there is also sex-linked inheritance. Indeed, if many genes underlying sexual dichromatism are not sex linked (Badyaev, 2002), sex linkage (**i.e., the fact that the phenotypic expression of an allele is directly tied to the sex chromosomes**) could also partially explain sexual dichromatism (Husby, Schielzeth, Forstmeier, Gustafsson, & Qvarnström, 2013; Larsen, Holand, Jensen, Steinsland, & Roulin, 2014). For instance, Z-linked genetic variance explained more of the total phenotypic variation in white wing patch size than did autosomal genetic variance (11% versus 40%) in the collared flycatcher, *Ficedulla albicollis* (Husby, et al., 2013). However, the contribution of such sex-linked variance to phenotypic variation is generally thought to be weak, although studies may have lacked sufficient power to distinguish autosomal genetic variance from sex-linked genetic variance (Charmantier, et al., 2017; Husby, et al., 2013). Furthermore, very few studies have yet attempted to estimate the Z-linked or W-linked heritability of coloration (Evans, Schielzeth, Forstmeier, Sheldon, & Husby, 2014).

**(iii) Fitness-related traits:** phenotypic traits like female colorations evolve **under sexual, social, and/or natural selection** if they affect proxies of fitness. **We will review below the progress that has been made in understanding the strength of sexual, social and natural selection on coloration in female birds**

## **Progress in understanding the strength of sexual selection on coloration in female birds**

Under sexual selection, individuals compete for mates and/or the opportunity to fertilize their gametes, and differences in their relative success leads to variation in reproductive success (Andersson, 1994; Darwin, 1871). Sexual selection is expected to operate on female coloration traits if they affect an individual's chances of obtaining a mate(s) and producing offspring. In addition to mate number, mate quality may also play a role.

The strength of sexual selection is in consequence estimated **by two steps**: **first** it is needed to measure the correlation between variation in phenotype, (here female coloration) and variation in mating success and, **second**, the correlation between variation in the number of partners and variation in reproductive success (Anthes, Häderer, Michiels, & Janicke, 2017; Henshaw, Jennions, & Kruuk, 2018). **To estimate the correlation between variation in phenotype and variation in mating success**, the mating differential and gradients **as well as** opportunity for sexual selection are computed. Mating differential and gradients correspond **to** the covariance between trait values and mating success. Opportunity for sexual selection corresponds to the variance in mating success divided by the squared mean value of mating success for the population. This latter metric establishes an upper bound for the mating differential for a standardized trait. **To estimate the correlation between variation in the number of partners and variation in reproductive success**, a Bateman gradient is used. It quantifies the relationship between mate number and reproductive success (this approach thus does not provide information about the traits which are determinant for mating success).

**What do we know about the strength of sexual selection on female coloration in birds? To answer this question, we must first make a detour reviewing what is known about the Bateman gradient and opportunity for sexual selection in birds.** Janicke and colleagues (2016) **performed a meta-analysis that included all animal studies in** which the opportunity for sexual selection and the Bateman gradient had been calculated for both males and females. **This Janicke et al.**

2016's data set included 12 species of birds that are presented in Table 2. Table 2 shows that for each of these 12 bird species, the two metrics are male-biased but also that in most bird species the effect size for the female Bateman gradient is significantly positive in female birds suggesting that females benefit from multiple mating in these cases. A meta-analysis run on this table 2 (i.e. specific to bird species and not on the whole data set as in Janicke et al. 2016) shows the mean effect size (mean±SE) for the sex difference in opportunity for sexual selection (0.24±0.088); the sex difference in Bateman gradient (0.45±0.103) and the female Bateman gradient (0.39±0.089). Table 2 also shows that these 3 metrics are all statistically significant (Janicke et al. unpublished data). Hare & Simmons (2019) mentioned two additional bird species: the black-legged kittiwake, *Rissa tridactyla* (Coulson & Thomas, reported in Clutton-Brock, 1983) and the house wren, *Troglodytes aedon* (Whittingham & Dunn, 2004). For these two monogamous species, the opportunity for sexual selection was also low, but never absent, in females compared to males, especially in the colonial monogamous bird (the kittiwake).

(Table 2 about here)

Could mating system explain some of the variability in Bateman gradient? In polygamous bird species, a steep and positive Bateman's gradient was found for the females of one brood parasite species: the great-spotted cuckoo, *Clamator glandarius* (Bolopo et al., 2017). In the brown-headed cowbird, *Molothrus ater*, the results are opposite as gradient is greater in males (Louder, Hauber, Louder, Hoover, & Schelsky, 2019) but see (Woolfenden, Gibbs, & Sealy, 2002). In polygynandrous species, positive Bateman gradients were seen in female red junglefowl (Collet, Dean, Worley, Richardson, & Pizzari, 2014) and female wild turkeys, *Meleagris gallopavo* (Krakauer, 2008). However, the gradient was only statistically significant in the red junglefowl. In contrast, in territorial and socially monogamous species, the gradients were less pronounced and different between the sexes. They were slightly positive overall in females (even if the statistical support was weak). This finding was found in the blue tit (García-

Navas et al., 2013; Schlicht & Kempenaers, 2013), the dark-eyed junco, *Junco hyemalis* (Gerlach, McGlothlin, Parker, & Ketterson, 2012), the hihi, *Notiomystis cincta* (Walker, Ewen, Brekke, & Kilner, 2014)), the mountain bluebird, *Sialia currucoides* (Balenger, Scott Johnson, Mays Jr, & Masters, 2009), and the white-crowned sparrow, *Zonotrichia leucophrys* (Poesel, Gibbs, & Nelson, 2011). Interestingly in addition, in two species of Darwin finches (*Geospiza fortis* & *G. scandens*) for which mating patterns change when environmental fluctuations alter sex ratios, females of both species were more frequently polyandrous in male-biased populations, and fledged more offspring by changing mates (Grant & Grant, 2019). Lastly, in cooperative breeding species, a positive Bateman gradient was found in females but not in males for the superb starling, *Lamprotornis superbus* (Apakupakul & Rubenstein, 2015). Taken together these findings indicate that positive Bateman gradients have been found in female birds, so mating with more mates may increase reproductive success in some species. They also indicate that gradient occurrence and strength could change according to mating system and environmental conditions.

The suggestion that mating system affects sexual selection estimates in bird is supported by the work of (Hauber & Lacey, 2005), who calculated sex-specific “measures of relative reproductive variability” between males and females for eight cooperative breeding species, and found that the value of this proxy of opportunity for selection (i.e., variance in relative reproductive success) was greater in females than males in five of these species. These five species are the brown jay, *Cyanocorax morio* (Williams, 2004), the white-browed scrubwren, *Sericornis frontalis* (Whittingham, Dunn, & Magrath, 1997)), the Arabian babbler, *Turdoides squamiceps* (Lundy, Parker, & Zahavi, 1998), the superb fairywren, *Malurus cyaneus* (Double & Cockburn, 2003), and the bicolor wren, *Campylorhynchus griseus* (Haydock, Parker, & Rabenold, 1996). It was identical for males and females in the red-cockaded woodpecker, *Picoides borealis* (Haig, Walters, & Plissner, 1994) and the Florida scrub jay, *Aphelocoma*

*coerulescens* (Fitzpatrick & Woolfenden, 1988) and was lower in females than males in the Seychelles warbler, *Acrocephalus sechellensis* (Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001). However, opportunity for selection is often considered to be the metric with the loosest link to sexual selection and few species are included (8), so more research is needed to confirm this bias in sexual selection for cooperative breeding species.

Several researchers (e. g. Anthes, et al., 2017; Collet, et al., 2014; Gerlach, et al., 2012) have pointed that positive Bateman gradients in females could be biased because more fecund females may be more attractive mates to males, such that many males choose to copulate with those fecund females. This would lead to a positive relationship between mating success and fecundity without any other causal relationship coming into play (i.e., females would not gain fitness benefits-i.e. no additional or better-quality nestlings- from having multiple mates). This argument is worth considering (and should also be systematically applied to sperm limited males who may have higher Bateman gradients when they produce more sperm). Recent papers have presented possible methods for dealing with this problem and for quantifying the strength of sexual selection (Anthes, et al., 2017; Henshaw, et al., 2018). Henshaw and colleagues (2018) propose for instance a method, based on a single path analysis model that includes how traits influence mating success and how mating success influences fitness.

In regard to the relationship between coloration and mating success in females (i.e. mating differential and gradients), we recommend referring to the recent review of (Hare & Simmons, 2019). However, we need to stress out that if the existing research quantifying the link between female coloration and mating success is most often performed in short-term studies. Using long-term data, ideally lifetime reproductive success, is needed to address identified issues related to randomness created by variation in environmental conditions and sampling (Clutton-Brock & Sheldon, 2010; Cockburn, 2014). It is important to note that these issues are also a problem

when characterizing how sexual selection affects male coloration in natural populations (Chaine & Lyon, 2008; Robinson, Sander van Doorn, Gustafsson, & Qvarnström, 2012).

Lastly for birds, a particularity is that many species present short- or long-term monogamy (Kvarnemo, 2018). A common expectation is that monogamy leads to little or no sexual selection. However, as pointed by (Kvarnemo, 2018), sexual selection can be substantial even under mutual monogamy, as mate quality is obviously more important than mate numbers, which in turn increases the strength of the pre-mating mate choice which can be associated with high variation in reproductive success (Hooper & Miller, 2008; A. G. Jones & Ratterman, 2009). More research is needed to quantify mating gradients and understand how sexual selection is working in those long-term monogamous species.

Overall, this section shows that in birds, males tend to have steeper indices of sexual selection (probably due to the taxon's high level of extrapair mating). However, there is also evidence that females have statistically significant positive estimates too. Furthermore, it seems that the occurrence and strength of estimates of sexual selection in males and females might vary according to mating system and degree of sociality. However, because we have still too few species for which sexual selection estimates has been computed, this conclusion requires confirmation. We therefore call for more research into defining mating gradient, opportunities for sexual selection and Bateman gradients for both sexes in birds and agree with the recent review of Kvarnemo (2018) that sexual selection in long-term monogamous birds need more studies.

### **Progress in understanding the strength of social selection on female coloration in birds**

Under social selection *sensus lato* any trait involved in competitive social interactions among individuals (Lyon & Montgomerie, 2012) affects fitness, which means that social selection *sensus lato* encompasses sexual selection. Social selection on female coloration may occur if social interactions favor female coloration phenotypes that enhance success in acquiring or



maintaining any reproductively valuable resource. Both positive and negative social interactions (i.e., cooperation versus competition) can lead to variation in reproductive success and survival and thus influence selection.

It is hard to find cases where the strength of social selection has been quantified in females and/or for female traits. The opportunity for social selection arises whenever reproductive success and/or survival vary among individuals as a direct result of interactions with conspecifics of the same or opposite sex (Wolf, Brodie & Moore, 1999). Traits affected by social selection are shaped by the beneficial (positive) or harmful (negative) effects of other individuals (McDonald, Farine, Foster, & Biernaskie, 2017). For instance, female coloration can play a determinant role in competition for resources (see section 4.2. below), which can be intense in females (Tobias, et al., 2012). Female coloration might also influence male behavior after pairing. A recent theoretical study showed that exaggerated mutual displays performed after mating could evolve via social selection if they increase parental investment, implying that mate stimulation could explain the presence of socially selected traits in females (Servedio, Price, & Lande, 2013). This finding could provide an evolutionary explanation for the coloration traits displayed by both sexes or just by females after mating. Emblematic examples include the dance performed by the blue-capped cordon-bleu, *Uraeginthus cyanocephalus* (Ota, Gahr, & Soma, 2015) and egg coloration (Moreno & Osorno, 2003).

Tools exist to measure social selection. The presence of social selection can be tested for using multilevel selection analysis, which builds on the classical Lande selection model (Lande & Arnold, 1983) by including the traits of social partners in addition to the traits of focal individuals (McDonald, et al., 2017). This approach partitions the fitness contributions of each individual to determine how specific traits involved in interactions influence selection strength. For instance, support for social selection has been found in great tits for arrival date: individuals that arrive late to the breeding site increase their probability of successfully acquiring a breeding

territory if they associate with other late-arriving conspecifics (Farine & Sheldon, 2015). Indirect phenotypic effects (i.e. effect of the genotype of an individual on the phenotypic trait value of another individual) have been found to explain a large proportion of the variation in female breeding date in American red squirrels (*Tamiasciurus hudsonicus*), although the specific traits of female neighbors that mediate this indirect effect have not yet been identified (Fisher et al., 2019). These multilevel methods (Fisher, et al., 2019; McDonald, et al., 2017) could and should be used to determine whether social selection has influenced female (and/or male) coloration and constitute a promising line of future research. For instance, it would be important to test whether including color traits from neighboring females in addition to color traits of focal females in a classical Lande selection model would influence the reproductive success of focal females.

### **Progress in understanding the strength of natural selection on female coloration in birds**

Natural selection *sensu stricto* could act on female coloration if coloration is linked to reproductive benefits and affects chances of survival; natural selection *sensu lato* encompasses both sexual and social selection.

Research measuring the strength of natural selection *sensu lato* acting on female coloration in birds is much more common than research measuring the strength of sexual and social selection; even if, unfortunately, such information on female coloration and fitness is not yet routinely obtained in most longitudinal studies. Generally, the relationship between phenotypes and fitness can be characterized using the classical Lande model mentioned above (Lande & Arnold, 1983; Morrissey & Sakrejda, 2013), which estimates covariance between traits and fitness (reproductive success or survival). This method requires long-term data for both variables. A classical quantitative genetics approach that directly estimates genetic covariance between traits and fitness may also be useful in this context (Charmantier, Garant, & Kruuk, 2014). Many studies could be mentioned but it is worth mentioning three recent studies

conducted at the phenotypic level that used large sample sizes collected across several years. In the common kestrel (*Falco tinnunculus*), positive directional selection was found to operate on the yellow chromaticity of the eye ring when number of fledglings served as the proxy for female fitness. This relationship was not present in males (Vergara, et al., 2015). In the prothonotary warbler (*Protonotaria citrea*), females with higher carotenoid levels in their crown feathers produced a greater number of fledglings (Bulluck et al., 2016). In the sociable weaver (*Philetarius socius*), viability selection (which operates on survival probabilities) was found to have an influence on female and male melanin bib size (Acker et al., 2015).

**Summary** - To conclude this section, it shows first that tools are available for measuring the influence of sexual, social and natural selection on female coloration in birds. It also points that these tools are still poorly used and that they require long-term data from natural populations. Such data set are scarce for females because their coloration traits are not systematically [measured](#) in long-term studies. Shorter-term experiments would also be of interest. For example, ecological factors such as density (Aronsen, Berglund, Mobley, Ratikainen, & Rosenqvist, 2013), food availability (Janicke, David, & Chapuis, 2015) or sex ratio (Grant & Grant, 2019) could be modified to test how environmental conditions affect the opportunity for sexual and social selection in females.

## 5. Signaling content of female coloration traits in birds

Determining the signaling content of female ornaments is an important step in understanding how and why this information is used by conspecifics. This step will allow here to address the following key questions: (i) could signaling costs constrain the evolution of female coloration in birds? (ii) What direct benefits males may acquire by choosing more colored females? and (iii) do female coloration traits in birds represent badges of status and why?

### **(i) Cost as a constraint in the evolution of female coloration?**

Emitters and receivers may have different interests. In birds, same-sex individuals display signals during competition for food and/or mates, and males and females interact to choose or to be chosen as a mate. Under such circumstances, signals must be reliable **to be used by the receivers** (Searcy & Nowicki, 2005). The condition-dependence/handicap hypothesis assumes that signals need to be costly to be reliable (Grafen, 1990; Zahavi, 1975). It follows that only high-quality individuals (e.g., those who are strong or in good condition) should be able to bear the cost of maintaining the most elaborate ornaments.

Signaling costs are often viewed as constraints on the evolution of ornaments in the sex that pays the greater cost of offspring production (i.e., generally female: Chenoweth, Doughty, & Kokko, 2006; Cuervo, Møller, & de Lope, 2003; Fitzpatrick, et al., 1995). Indeed, female reproductive fitness is likely to be more resource limited, and females investing in costly sexual traits may have decreased fecundity. In contrast, a similar investment by males is unlikely to impact their reproductive capacities. However, **are signaling costs really constraining the evolution of color ornaments in females?** What do we actually know about the cost of female **color** ornaments and its effect on reproductive investment in females? **Could** this trade-off be minimized or circumvented?

**First, the trade-off could be minimized or circumvented if color production is temporally decoupled from reproductive investment.** In the case of plumage coloration, a trade-off between coloration and investment in offspring in females could be avoided because plumage is inert after it has been produced (i.e., **after** molting), and **so** coloration is in place long before the breeding season starts in some species. For instance, in most European passerines, plumage is renewed after the breeding season, so it is unlikely that two events separated by more than nine months would be involved in a trade-off **decreasing female future capacity to invest in reproduction**. In the case of bare-part coloration and cosmetic coloration,

costs might be also minimized if investment in coloration only takes place when an individual needs to signal (see below the example of the flamingo coloration). Bare body parts are caruncles, legs, eye rings, or bills, they are living tissues whose color can change within a few days following food deprivation or immune challenge (Faivre, Gregoire, Preault, Cezilly, & Sorci, 2003; Iverson & Karubian, 2017; Rosenthal, Murphy, Darling, & Tarvin, 2012; Velando, Beamonte-Barrientos, & Torres, 2006). Cosmetic coloration occurs when an external substance is applied to plumage (Delhey, Peters, & Kempenaers, 2007). The greater flamingo (*Phoenicopterus roseus*) provides an interesting example of cosmetic coloration displayed only when needed. This monogamous species displays reversed sexual dichromatism even though it has conventional sex roles and male-biased size dimorphism (Perez-Rodriguez, Mougeot, & Bortolotti, 2011). The degree of coloration depends on the concentrations of carotenoids in uropygial secretions, and carotenoid levels in uropygial secretions are higher during mate choice than during chick provisioning. Additionally, carotenoid concentrations in uropygial secretions do not reflect carotenoid concentrations in plasma. This example illustrates well that resources invested in signaling can be allocated rapidly based on need, a flexibility that makes cost-based constraints on the evolution of coloration less likely (Amat et al., 2018).

**Second, different signals may have different costs, and females may preferentially display ornaments that are less costly.** In accordance with the condition-dependence/handicap hypothesis (Grafen, 1990; Zahavi, 1975), ornaments must have a cost to evolve into signals. However, according to the aesthetic evolution hypothesis (Hill, 2015; Price, Stoddard, Shevell, & Bloch, 2019; Prum, 2012; Renoult, Bovet, & Raymond, 2016; Renoult & Mendelson, 2019), cost is not a prerequisite. Traits can evolve simply as a result of sensory bias or because they allow quicker cognitive evaluation by receivers (Renoult & Mendelson, 2019). They might also evolve because of the runaway hypothesis (Kirkpatrick, 1982; Lande, 1981; Rosenthal, 2018). Consequently, secondary sexual ornaments can be sexy signals,

entirely arbitrary traits, *i.e.* characteristics that became successful just because they are preferred. Females may preferentially use this type of sexy signals.

To date, however, it remains unclear which color ornaments are more likely to be free of cost. As mentioned earlier in this review, carotenoid-based colors may be more costly than other colors because they have tight metabolic links with important cellular processes (Hill & Johnson, 2012). A recent meta-analysis (Weaver, Santos, Tucker, Wilson, & Hill, 2018) supported this idea and further showed that colors based on converted carotenoids are linked to proxies of individual quality, more than colors based on dietary carotenoids (dietary carotenoid such as lutein and zeaxanthin are present in food and are deposited unchanged in the feathers; converted carotenoids are derived from dietary carotenoids and are biochemically converted before deposition). By contrast the only meta-analysis that compared carotenoid-based plumage and melanin-based plumage colors found the same condition dependence for both type of coloration (Griffith, Parker, & Olson, 2006), but in this analysis the different types of carotenoids were not differentiated. In relation to structural coloration, although some authors have argued that structural coloration is not very costly (Prum, 2006), experiments have shown that structural coloration can be affected by an individual's condition (Doutrelant, Grégoire, Midamegbe, Lambrechts, & Perret, 2012; Hill, Doucet, & Buchholz, 2005; McGraw, Mackillop, Dale, & Hauber, 2002; but see: Peters, Kurvers, Roberts, & Delhey, 2011; Siefferman & Hill, 2005b; Siitari, Alatalo, Halme, Buchanan, & Kilpimaa, 2007). Additional research is therefore needed to understand if coloration types differ in their costs and whether such costs are directly defined by production (e.g., as proposed for carotenoid-based colors) or indirectly defined by the risks associated with conspicuous display (Delhey, Szecsenyi, Nakagawa, & Peters, 2017).

To date, only a few experiments have been performed to test the costs of coloration in females. They have found that female coloration is sensitive to the availability of food resources

(Morales, Velando, & Torres, 2009; Siefferman & Hill, 2005a) and greater reproductive costs (Doutrelant, et al., 2012). In the common waxbill (*Estrilda astrild*), favorable environmental conditions (higher nighttime temperatures) were found to positively affect red bill coloration in females: both sexes had similar bill coloration when nighttime temperatures were high but only males had redder beaks under most conditions (Funghi, Trigo, Gomes, Soares, & Cardoso, 2018).

To determine which coloration types might be more or less costly, it is essential to conduct experiments on both sexes within a species (Doutrelant, et al., 2012). This approach makes it possible to compare how different coloration traits respond to the same experimental treatments (Hill, Hood, & Huggins, 2009; Peters, Delhey, Andersson, van Noordwijk, & Forschler, 2008; Siefferman & Hill, 2005b); ideally, both sexually selected and non-sexually selected traits would be included (Cotton, Fowler, & Pomiankowski, 2004). To our knowledge, this type of experiment has never been done. Additionally, data on different coloration traits from long-term studies are invaluable because environmental fluctuations result in somewhat variable conditions (Cockburn, Osmond, & Double, 2008; Vergara, Mougeot, Martínez-Padilla, Leckie, & Redpath, 2012) and studies carried out over extended time periods are like natural experiments (or pseudo-experiments). Ideally, such long-term studies should examine both sexually and non-sexually selected traits.

**Third, females may preferentially use badges of status which are viewed as ornaments with social costs but with no production costs. The social costs given by the** receivers who attack emitters displaying similar signal levels are maintaining signal honesty (Maynard-Smith & Harper, 2003). **In this case, there would thus be no trade-off between coloration cost and future female fecundity, and females could be more unconstrained in their use of badges of status in competitive interactions. These badges of status should be quite frequent in females.** Research in American goldfinches (*Spinus tristis*) found evidence for the badge-of-status

hypothesis: in females, bill coloration was not affected when flying capacity was experimentally impaired. However, it was impacted when social costs were experimentally increased (i.e., artificially creating winners and losers during social interactions leads to respectively increase bill coloration in winners and decrease coloration in loser: Tarvin et al., 2016a). A comparative study found a similar result: carotenoid-based bill coloration seemed to be more correlated with indices of sociality (sociality over the winter, coloniality) than with indices of sexual selection (Dey, Valcu, Kempenaers, & Dale, 2015).

**Fourth, costs may be offset by benefits and costly female ornaments be present whenever benefits of displaying the signals are important.** Costs do not exist in isolation (Cain & Rosvall, 2014), so they must be associated with benefits. Males investing more in parental care are predicted to be choosier. As a result, if a female's investment in coloration is rewarded by a greater chance of acquiring a highly investing male or by enhancing parental care coordination between partners, then signaling costs may be offset. Support for this idea has been obtained in fishes (Méndez-Janovitz, Gonzalez-Voyer, & Macías Garcia, 2019): females were much more ornamented in a subfamily where males of the species invested heavily in reproduction (Goodeinae) than in a subfamily where they did not (Poeciliinae). In birds also, at the interspecific level, presence of parental care seems to be associated with more ornamented females (Dale et al. 2015). At the intraspecific level, the hypothesis above could be tested in birds by experimentally changing female coloration and determining whether highly ornamented females are chosen by better-quality males who have better territory or are better at taking care of the young. The differential allocation hypothesis which predicts that reproductive investment is influenced by mate attractiveness, also predicts such differences in investment in relation to female ornaments. The fact that more ornamented females have male capable of investing more have been observed in various species: for example, for sperm allocation in feral junglefowl (Pizzari, 2001), for nest defense in rock sparrows (Petronia



petronia Matessi, Carmagnani, Griggio, & Pilastro, 2009), or for feeding rate in tree swallow (*Tachycineta bicolor* Dakin, Lendvai, Ouyang, Moore, & Bonier, 2016) or mountain white-crowned sparrow (*Z. leucophrys oriantha*: Laubach, Perng, Lombardo, Murdock, & Foufopoulos, 2015). However not all studies found positive associations: (e.g. Berzins & Dawson, 2016; Limbourg, Mateman, & Lessells, 2013a), and a meta-analysis should be performed. In general, more experiments are needed to test this hypothesis. When mate choice is based on plumage coloration, experiments need to be performed before mate choice occurs because plumage coloration is not temporally dynamic. An experiment that manipulated plumage color after individuals had already paired would create unnatural conditions, which could explain the inconsistency in results found in several studies (e.g. Limbourg, Mateman, & Lessells, 2013b; Mahr, Griggio, Granatiero, & Hoi, 2012).

#### **(ii) Benefits of male mate choice**

To understand the evolution of female ornament through mate choice, it is needed to determine which benefits males may acquire when choosing a female based on their ornaments.

Direct benefits take place when mating with a high-quality partner increases male current reproductive success or survival. Indirect benefits occur when ornaments are heritable and when more ornamented females are linked to better quality genes. When direct benefits exist, male mate choice has been shown as an evolutionary stable strategy in both polygynous and monogamous species (Courtiol, Etienne, Feron, Godelle, & Rousset, 2016; Ihara & Aoki, 1999; Servedio & Lande, 2006). In contrast, in polygynous species when direct benefits are absent, and in species where there are pronounced sexual conflicts or sexual harassment on females, male mate choice is less likely to lead to the evolution of female-specific traits (Fitzpatrick & Servedio, 2017; Long, Pischedda, Stewart, & Rice, 2009). Additionally, papers suggest that, in polygynous species, male mate choice is less likely to evolve in the case of indirect benefits and arbitrary traits (Fitzpatrick & Servedio, 2018). This review also indicates that when mating

investment costs are low for males, indirect benefits are less likely to be maintained by selection and less likely to exceed the benefits of multiple mating. Clearly, understanding the overall benefits of male mate choice is key to understanding the evolution of female coloration.

The direct and indirect benefits obtained by females via mate choice have been thoroughly characterized. Thus, rather than simply listing similar benefits acquired by males who mate with high-quality females, we instead focus on direct benefits that are particularly exclusive to females and/or linked to female reproductive capacity.

**A direct benefit exclusive to female ornaments: enhanced fecundity.** In several bird species, different types of coloration have been shown to signal fecundity. For instance, in the sexually dichromatic upland goose (*Chloephaga picta leucoptera*), the reddish-brown coloration of the head and the yellow-orange coloration of the legs signal condition and fecundity (Gladbach, Gladbach, Kempnaers, & Quillfeldt, 2010). In the sexually monochromatic eastern bluebird (*Sialia sialis*), females with more pronounced chestnut plumage produce larger clutches (Grindstaff, Lovern, Burtka, & Hallmark-Sharber, 2012). Also, based on the results of a ten-year study in the common kestrel, the gray coloration of the rump appears to be correlated with clutch size in females (Vergara, Fargallo, Martinez-Padilla, & Lemus, 2009). Experimental studies are less common, but they too suggest that female coloration is linked with egg production capacity. When feral pigeons (*Columba livia*) were subject to food restrictions, darker eumelanic females had higher egg production levels (Jacquin, Récapet, Bouche, Leboucher, & Gasparini, 2012); a similar result was found for yellow brightness in an experiment in blue tits where females were forced to lay a second clutch (Doutrelant et al., 2008). However, not all studies have found a positive relationship between female coloration and fecundity. A meta-analysis focused on this question is needed if we wish to determine the strength of this relationship and to determine if some coloration types are more tightly linked to fecundity than others.

**An important direct benefit linked to female reproductive capacity: stress resistance.**

Resistance to stress is another quality that males may look for in females. Indeed, stress-sensitive females are more likely to abandon their nestlings. Support for this idea was found in an experiment in tree swallows where wing feathers were bound together to reduce wing surface, hence birds were reversibly handicapped to mimic stressful conditions: females with brighter white breasts were less likely to abandon their nests (Taff, Zimmer, & Vitousek, 2019). Coloration has been found to signal stress resistance in many species, an association that could be due to diverse mechanisms stress hormones might affect physiological trade-offs involving for instance immune responses, but also regulation of energy intake, feather quality due to change in moult speed induced by change in corticosterone level, and / or on contrary the effect of signals on stress level (DesRochers et al., 2009; Kennedy, Lattin, Romero, & Dearborn, 2013; Romero, Storchlic, & Wingfield, 2005). So far, both negative and positive associations have been found for carotenoid-based coloration and levels of corticosterone in the blood or feathers. For instance, yellow coloration was negatively linked to feather corticosterone in females but not in old males yellow warblers (*Setophaga petechia*: Grunst, Grunst, Parker, Romero, & Rotenberry, 2014). By contrast, the feather corticosterone of common redpolls (*Acanthis flammea*) was positively correlated with carotenoid pigmentation in adult males but not in females or younger males (Fairhurst, Dawson, van Oort, & Bortolotti, 2014). In studies that only include males, both negative and positive correlations have also been found (negative: Kennedy, et al., 2013; Mougeot, Martinez-Padilla, Bortolotti, Webster, & Piertney, 2010; positive: Fairhurst, Damore, & Butler, 2015; Lendvai, 2013 #4768; Fairhurst, et al., 2014). Mostly negative correlations have been reported for structural coloration, both in female and male eastern bluebirds (Grindstaff, et al., 2012) and in female blue tits (Henderson, Heidinger, Evans, & Arnold, 2013; but not in female tree swallows: Sarpong et al., 2019). Clearly, to better characterize the relationship between stress resistance and coloration in females (and

males), we need experimental studies like those performed in crimson rosella (*Platycercus elegans*) males (e. g. Berg, Knott, Ribot, Buchanan, & Bennett, 2019) where stress-induced corticosterone predicted change in pigment- and structural-based coloration after molting.

**A direct benefit exclusively to female ornaments: the advantages associated with maternal effects.** Maternal effects are non-genetic mechanisms by which females can influence the phenotype and fitness of their offspring (Mousseau & Fox, 1998). There are two categories: prenatal maternal effects and postnatal maternal effects. We will first address postnatal maternal effects, which arise from maternal care, namely providing food, clean nest conditions, and protection from predators. Postnatal maternal effects obviously play a determinant role in offspring survival and fitness and thus their relationship with maternal coloration is frequently examined. For instance, in the sexually dichromatic northern cardinal (*Cardinalis cardinalis*), female underwing color and face mask size were both found to be positively related to maternal care (Jawor, Gray, Beall, & Breitwisch, 2004). In eastern bluebirds, maternal provisioning behavior was positively associated with female rump color (Siefferman & Hill, 2005a). By contrast, in the American redstart (*Setophaga ruticilla*), females with brighter yellow tails visited their nests less frequently (Osmond et al., 2013).

Prenatal maternal effects involve the passive or differential allocation of nutrients and/or substances that affect embryonic development and/or offspring development (Badyaev, 2008; Blount, Houston, & Møller, 2000; Sheldon, 2000). They are suspected to have a broad range of effects on offspring fitness. Although evidence for prenatal maternal effects has not been unequivocal in all studies (Henriksen, Rettenbacher, & Groothuis, 2011), we can nonetheless state that such effects can play a decisive role in offspring fitness in some species and/or in certain environments because they help offspring face harsh conditions. Egg size is an example of a prenatal maternal effect (Krist, 2011; Williams, 1994) and was positively correlated with

ornamentation in feral female junglefowl: females with larger combs laid heavier eggs (Cornwallis & Birkhead, 2007).

Other examples of prenatal maternal effects include the compounds found in egg contents, such as carotenoids (Biard, Surai, & Møller, 2005; McGraw, Adkins-Regan, & Parker, 2005). Carotenoid levels in the yolk play a crucial role in offspring health, survival, growth, and fledging success (Biard, et al., 2005; Blount, 2004; McGraw, et al., 2005). For instance, higher levels of carotenoids in eggs enhance the immune response of offspring (Biard, Surai, & Møller, 2007; Saino, Ferrari, Romano, Martinelli, & Moller, 2003) and can compensate for the negative effects of ectoparasitism (Ewen et al., 2009). It has been hypothesized that if coloration indicates female quality, then less colored females—but not highly colored females—might have to trade off between transmitting carotenoids to their eggs and keeping carotenoids for themselves. In agreement, a positive relationship between egg carotenoid levels and female coloration was observed in experimental studies on the black-backed gull, *Larus fuscus* (Blount et al., 2002), the zebra finch (McGraw, et al., 2005), and the blue tit (Midamegbe et al., 2013). Results from correlative studies are more mixed. For instance, on the one hand, egg carotenoid content was correlated with the immaculateness of the white cheek patch in female great tits (Remeš et al. 2011) and the number of spots in female diamond firetails, *Stagonopleura guttata* (Zanollo et al., 2013), but on the other hand, there was no correlation between egg carotenoid content and carotenoid-based coloration in female blue tits or great tits (Biard, et al., 2005; Remeš, Matysioková, & Klejdus, 2011; Szigeti et al., 2007).

Females also transfer antibodies to their eggs, and these antibodies are essential in protecting nestlings during their first days of life (Boulinier & Staszewski, 2008; Hasselquist & Nilsson, 2008). There may even be a transgenerational impact; one experimental study in urban pigeons found that maternal effects carried all the way through to grandchildren (Ismail, Jacquin, Haussy, Perret, & Gasparini, 2015). To date, to our knowledge, only two experiments have

examined the link between plumage coloration and antibody transfer capacity in females. In the first study, when feral female pigeons were injected with inactivated *Chlamydia psittaci* (a natural bacterial pathogen), darker mothers transferred more antibodies against the bacterium into their eggs than did paler ones, even though their levels of circulating antibodies were similar (Jacquin, Haussy, Bertin, Laroucau, & Gasparini, 2013). In barn swallows (*Hirundo rustica*), darker females allocated more antibodies to their eggs, but only when their offspring sex ratio was female-biased (Saino et al., 2014). Because melanogenesis and immunity are partly genetically controlled (Ducrest, Keller, & Roulin, 2008), parental melanin-based pigmentation may covary with the levels of immune factors transferred to eggs. In addition, correlations between eggshell coloration and antibody levels have been found in the pied flycatcher (*Ficedula hypoleuca*) and the blue tit (Holveck et al., 2012; Morales, Sanz, & Moreno, 2006).

Lastly, maternally derived steroids (i.e., testosterone, 4-androstenedione) and corticosterone (Gil, 2008; Groothuis, Müller, von Engelhardt, Carere, & Eising, 2005; Schwabl, 1993) are also present in the egg yolk and result in key maternal effects. The transfer of corticosterone is assumed to be passive (Hayward & Wingfield, 2004) and thus directly [linked to female stress level](#). A recent meta-analysis of 117 studies that experimentally modified hormones in females before they laid eggs or in the eggs themselves prior to incubation, confirmed that maternal androgens affect offspring development and, more specifically, offspring dominance and competitive ability (Podmokła, Drobniak, & Rutkowska, 2018). Testosterone and androstenedione can increase begging behavior, growth, and survival during early life (Groothuis, Muller, von Engelhardt, Carere, & Eising, 2005). However, they may also have negative effects, for instance yolk androgens reduce survival in American kestrels (*Falco sparverius*) (Sockman & Schwabl, 2000). Similarly, excessively high corticosterone levels can reduce hatchling size and begging behavior (Saino, Romano, Ferrari, Martinelli, & Moller,

2005). Prenatal hormones can also have long-lasting effects on offspring phenotypes and fitness that impact dispersal behavior, survival (Tschirren, Fitze, & Richner, 2007), adult immunity (Tobler, Hasselquist, Smith, & Sandell, 2010), and metabolic rate (Nilsson, Tobler, Nilsson, & Sandell, 2011). Transgenerational effects, stretching from females to their grandchildren, have also been observed (Khan, Peters, Richardson, & Robert, 2016);(Podmokła, et al.). For instance, maternal hormones seem to affect the reproductive investments made by female offspring (Hsu, Dijkstra, & Groothuis, 2016; Müller, Vergauwen, & Eens, 2009; Podmokła, et al., 2018). Consequently, [because](#) maternal hormones and nutrients in eggs have complex effects that can only be detected in specific environmental contexts (Groothuis & Taborsky, 2015; Morosinotto et al., 2013), it is important to carry out more correlative and experimental studies that test whether maternal coloration can signal the ability to transfer maternal hormones, and how such maternal effects influence offspring development.

### **(iii) Female-female competition and female coloration**

**Experimental evidence for badges of status in birds.** With badges of status, competitors can evaluate each other's competitive abilities from a distance, and conflicts can be resolved without paying high costs of fighting when signalers display badges of different sizes or intensities (Rohwer, 1975, 1977). Badges of status have mainly been described in males (Santos, Scheck, & Nakagawa, 2011; Senar, 2006), but [description of female badges of status is growing in literature](#). Female birds of many species compete for food and/or territories before or during the breeding season (Stockley & Campbell, 2013; Tobias, et al., 2012). Some authors have suggested that females may compete more between each other than males before the breeding season. This would explain why in American goldfinches, bill color seems to function as a badge of status in females but not in males (Murphy et al., 2014). That said, we still have limited experimental evidence indicating that coloration plays a role in female-female competition. Our survey of the literature for birds found 16 species for which experimental

studies had been performed (Table 3). For instance, in the female pied flycatcher, decreasing the size of the white wing patch reduced female incubation attendance, a result thought to be the results of their decreased status (Plaza, Cantarero, Cuervo, & Moreno, 2018), or in the lovely fairywren (*Malurus amabilis*), less colored females (and males) reacted more aggressively when shown images of themselves than when shown images of more colored birds (Leitão, Hall, Delhey, & Mulder, 2019). In prothonotary warblers, nest boxes were placed in high and low quality territories and it appeared that older females with purer yellow breast coloration occupied nest boxes in higher quality territories (Beck, 2013). Most of the experimental studies listed in Table 3 yielded results that support the badge-of-status hypothesis. However, some are based on small sample sizes, and it is important to acknowledge that many negative results might have gone unpublished (Sanchez-Tojar et al., 2018). It is thus necessary to continue conducting experimental studies on a larger number of species, with adequate sample sizes and methods (Chaine, Shizuka, Block, Zhang, & Lyon, 2018). More tests are particularly important because social and intersexual selection are thought to be the most powerful selective forces acting on female ornaments (Stockley & Campbell, 2013; Tobias, et al., 2012).

(Table 3. about here)

**Is there a specific coloration type associated with badges of status and, if so, why?** Based on Table 3, it appears that all types of coloration can act as badges of status in females, for example, five species had carotenoid-based badges of status, three had melanin-based badges of status, and seven had structural-coloration-based badges of status. For coloration traits to serve as badges of status, they need to reflect condition, dominance or aggressiveness. Association between (i) condition, (ii) dominance or aggressiveness have been found for all type of colorations. (i) Condition - as stated earlier in the review, experiments have shown that iridescent and dark structural coloration is affected by bird condition (Doutrelant, et al., 2012; Hill, et al., 2005; McGraw, et al., 2002; but see Peters, et al., 2011; Siefferman & Hill, 2005b;



Siitari, et al., 2007). White feathers could also convey condition at molting, since their lack of melanin may make them more sensitive to wear and more vulnerable to parasites and bacteria, especially when feather quality is low (Ruiz-De-Castañeda, Burt, González\_Braojos, & Moreno, 2015; Swaddle & Witter, 1995). As also stated earlier in the text, carotenoid-based coloration (i.e., yellow, orange, red) reveals condition because carotenoids must be acquired from the environment, notably from food resources, and because they are used in other physiological processes, such as detoxification and immune function (Simons, et al., 2012). For instance, in the red grouse (*Lagopus lagopus scoticus*), female comb brightness and size were inversely correlated with parasite load (Martinez-Padilla et al., 2011). ii) **Aggressiveness and dominance**- testosterone which is often linked to dominance and aggressiveness is linked to a wide range of coloration traits, as well as badge-of-status size, in females. In experimental studies, increasing testosterone has induced male-like patterns of carotenoid-based coloration (Lahaye, Eens, Darras, & Pinxten, 2014; McGraw, 2006) and structural coloration in females (Peters, 2007). For melanin coloration this was not the case (Anthes, et al., 2017; Strasser & Schwabl), however in the white-shouldered fairywren (*Malurus alboscapulatus*), it has been proposed that there is a link between testosterone and melanin-based coloration because in populations where females are more colored, females are also more aggressive and have higher levels of circulating testosterone (Enbody, Boersma, Schwabl, & Karubian, 2018). Such a relationship with testosterone also seems to exist for melanin-based coloration within populations of North American barn swallows, *Hirundo rustica erythrogaster* (Vitousek, Stewart, & Safran, 2013); for carotenoid-based coloration in American goldfinches (Pham, Queller, Tarvin, & Murphy, 2014), and for white structural coloration in pied flycatchers (Cantarero et al., 2017; Moreno, Gil, Cantarero, & López-Arrabé, 2014). In the case of melanin-based coloration, this link may result because of pleiotropic genes that produce proteins involved in both melanin production and androgen production (Ducrest, et al., 2008). For

carotenoid-based coloration, testosterone has been found to increase carotenoid bioavailability (Blas, Perez-Rodriguez, Bortolotti, Vinuela, & Marchant, 2006; McGraw, 2006). In contrast, the proximate links between structural coloration and testosterone are less clear, but some research has found that manipulating testosterone levels in males can change their coloration (Peters, Delhey, Goymann, & Kempenaers, 2006; Roberts, Ras, & Peters, 2009). So the links between female coloration and badges of status can be explained because they have increased condition and/or testosterone level.

Historically, the byproduct hypothesis was used to explain the correlation between female ornamentation and testosterone (Kimball & Ligon, 1999). In the same time, it served to explain that evolution of female ornamentation was constrained. Like males, females with higher testosterone levels would invest less in offspring care (e. g. Clotfelter et al., 2004; Gerlach & Ketterson, 2013). However, the effects of testosterone may be limited because testosterone levels often decline when the demands of offspring increase.

Finally, the fact that coloration traits can function as badges of status could be explained by [their sensitivity](#) to social context (i.e., the sum of the social interactions experienced by an individual). Social context influence the physiology, behavior, and signaling traits of individuals, which induces feedback loops between signals and hormones (Vitousek, Zonana, & Safran, 2014). This has been shown in male white-crowned sparrows for which the size of the crown white patch signal an individual's ability to acquire resources, and experimental enhancement of the white patch increased baseline corticosterone levels (Laubach, Blumstein, Romero, Sampson, & Foufopoulos, 2013). Also in the North American barn swallow, males whose plumage had been darkened had higher levels of testosterone (Safran, Adelman, McGraw, & Hau, 2008). This species is sexually monochromatic, and, intriguingly, females whose plumage had been darkened displayed the opposite effect: they had lower levels of both circulating testosterone and plasma oxidative damage (Vitousek, et al., 2013). Clearly, more

research is needed on both sexes to understand this opposite effect. Also clearly to better understand how coloration could help mediate aggressive interactions among females, we need a better grasp of the physiological mechanisms that underlie aggressiveness in females.

**Physiological mechanisms underlying female aggressiveness.** As mentioned above, one hypothesis is that aggressiveness is driven by testosterone levels, like in males. In several species (Rosvall, Bentz, & George, 2019), such as the dark-eyed junco (Cain & Ketterson, 2012), females with experimentally heightened testosterone levels displayed more aggressive territory-defense behaviors. This relationship may arise because females have androgen receptors in brain regions associated with aggression (Rosvall et al., 2012). However, although long-term observational studies and natural experiments have shown that certain social conditions, such as higher breeding densities, are correlated with higher testosterone levels in females, the latter is not the systematic response to experimentally induced social challenges (Rosvall, et al., 2019). In addition it seems that testosterone is not responsible for all the similarities or differences between the sexes. For instance, a comparative study of 51 bird species found that high levels of testosterone in females were not related to variation in sexual size monomorphism, sexual plumage monochromatism, mating system, latitude, or the degree of coloniality (Goymann & Wingfield, 2014). Several studies (Goymann & Wingfield, 2014; Stockley & Campbell, 2013) have thus suggested that other mechanisms should also be examined, such as reduced testosterone sensitivity at neural sites associated with maternal behavior or sex-specific genomic responses to testosterone (Rosvall, 2013; Rosvall, et al., 2012). If aggression is regulated via sensitivity to sex-specific steroids, as opposed to via testosterone levels themselves, it could allow organisms to display aggressiveness while also avoiding the costs associated with systemically high testosterone levels. Interestingly, Rosvall et al. (2019) advocates taking a further step: replacing classical indices of male-male competition and male-specific sexual selection with newly designed metrics that characterize

the strength of female-female competition (such as competition for nesting sites, high quality males, or the benefits they provide). This recommendation to move beyond the field's current research framework, which is based on studies of males, is strikingly similar to the conclusion we reached in our section reviewing comparative studies of female coloration.

**Summary** - To conclude this section on the signaling content of female coloration traits, it appears that much remains to be done for most of the topics addressed. There is a need to study physiological mechanisms that are specific to females while also exploring relationships between coloration and other traits in both females and males. As mentioned, this is valid for condition, aggressiveness, testosterone, and this seems also true for other important functions such as immune function (Kelly, Murphy, Tarvin, & Burness, 2012) or oxidative stress (Viblanco et al., 2016). In addition, questions should be more explored using experimental studies that include both females and males. Care should be taken to better represent complexity in the experiments. For example, a study could look at several traits at the same time in both sexes, and several types of experiments could be carried out in the same species. In the last part of this review, we will highlight why it is crucial to work extensively on a single study model and how such an approach will increase our scientific standards.

## 6. The blue tit as a model study system

The last part of this review is an overview of studies that have explored the evolution of female—and male—coloration traits in a single species, the blue tit (Table 4). Some of the studies are our own. Most research on female and male coloration in blue tits has focused on two coloration traits: the ultraviolet (UV)-blue crown and the yellow breast. The UV-blue coloration of the crown results from plumage macro- and microstructures (Hegyi et al., 2018; Jacot & Kempenaers, 2007). The yellow coloration of the breast is carotenoid-based (Partali, Liaaenjenen, Slagsvold, & Lifjeld, 1987) and may also be due to microstructure (Jacot,

Romero-Diaz, Tschirren, Richner, & Fitze, 2010; Shawkey & Hill, 2005). In addition to working on these two traits (Figure 2), we have also studied eggshell coloration.

Initial studies in the late 1990s revealed the bird's sexual dichromatism (Andersson, Örnberg, & Andersson, 1998; Hunt, Bennett, Cuthill, & Griffiths, 1998). Subsequently, a plethora of quality research was produced for males, and the results largely suggest that UV-blue crown coloration and yellow breast coloration are sexually selected (Alonso-Alvarez, Doutrelant, & Sorci, 2004; D'Alba et al., 2010; Delhey, Johnsen, Peters, Andersson, & Kempenaers, 2003; Delhey & Kempenaers, 2006; Delhey, Peters, Johnsen, & Kempenaers, 2006, 2007; Dreiss et al., 2006; Griffith, Ornberg, Russell, Andersson, & Sheldon, 2003; Kingma et al., 2009; Korsten, Lessells, Mateman, van der Velde, & Komdeur, 2006; Korsten, Vedder, Szentirmai, & Komdeur, 2007; Ornberg, Andersson, Griffith, & Sheldon, 2002; Parker et al., 2011; Peters, et al., 2006; Rémy, Grégoire, Perret, & Doutrelant, 2010; Roberts, et al., 2009; Senar, Figuerola, & Pascual, 2002; Sheldon, Andersson, Griffith, Ornberg, & Sendecka, 1999; Szigeti, et al., 2007; Vedder, Korsten, Magrath, & Komdeur, 2008; Vedder, Schut, Magrath, & Komdeur, 2009). However, a meta-analysis that looked at all the studies together found support for just a single conclusion: that blue tits have a sexually dichromatic blue crown that displays greater UV reflectance in males than in females (Parker, 2013). The equivocal nature of the results largely stems from small sample sizes [and inflated type I error rate](#), but might also partly be explained by the fact that the results came from different blue tit populations across Europe.

We have put together a summary of the different studies that have looked at female coloration in the blue tit (Table 4). Below, we discuss what we have gleaned from them about the potential for selective pressures to act on female coloration in this species.

**The heritability of coloration and the strength of inter-sex genetic correlations.** In previous research, we estimated the heritability of female and male coloration and the strength of related genetic correlations using quantitative genetics tools (Charmantier, et al., 2017). We

found a moderate level of heritability (around 15%) for the chromatic part of the coloration of both the UV-blue crown and the yellow breast, which is a bit higher than 0.07-0.10, the heritability found in a blue tit study population in the United Kingdom (Hadfield, et al., 2006). For the achromatic part (brightness) of both characteristics, we found little to no heritability, a result that was consistent with findings on yellow breast brightness in a great tit population in the United Kingdom (Evans & Sheldon, 2011). Our results also indicated that most of the genetic variation underlying coloration is shared by both sexes, a result that supports the existence of strong genetic correlations between sex-specific coloration traits (Charmantier, et al., 2017).

**The link between female coloration and maternal quality.** We have conducted experiments to better understand the relationship between female coloration and maternal investment in reproduction to determine whether maternal coloration could signal maternal quality. In a first experiment, we forced females to lay later in the season and found that, within this treatment group, there was a positive association between yellow breast brightness and the ability to lay a large clutch and recruit more offspring (Doutrelant, et al., 2008). No such relationship was found in the control group. We then conducted an experiment in which we provoked an immune response in females before they laid their eggs. In the treatment group, females with brighter yellow breasts transferred higher levels of carotenoids to their eggs (Midamegbe, et al., 2013); this relationship was not seen in the control group. We also found female yellow breast brightness to be positively correlated with egg antibody concentrations (Holveck, et al., 2012). Taken together, these results led us to conclude that yellow breast brightness could be a signal of maternal quality in blue tits. They also suggested that relationships between signals and quality in females may be easier to detect under adverse conditions. Interestingly, results from our long-term data set (which includes more than 15 years of data on female and male coloration) also indicate that there is spatiotemporal variation in relationships between

coloration traits and proxies of reproductive success. For example, the correlation between female coloration and clutch size fluctuates greatly [across years and among our populations from southern France](#) (Figure 3). Female ornaments were [also](#) found to be associated with proxies of maternal quality in certain other blue tit studies [throughout Europe](#) (Garcia-Navas, Ferrer, & Sanz, 2012; Henderson, et al., 2013; Szigeti, et al., 2007), but sometimes no such relationship was observed (Hadfield, et al., 2006; Lucass, Iserbyt, Eens, & Müller, 2016; Parker, et al., 2011). If female coloration signals quality, one should expect to see [positive associations](#) between proxies of female quality and male investment in parental care. In one study, carried out within a single population, males invested more when paired with females whose UV-blue crowns had greater UV reflectance, i.e., lower hue (Mahr, et al., 2012). However, in two other studies performed in another population, the opposite was found: males invested less when paired with females whose UV-blue crowns had greater UV reflectance (Limbourg, et al., 2013a, 2013b). Overall, this section shows that there is some support for the idea that female coloration signals maternal quality and a female's ability to invest in offspring, but it also supports the call by Parker (2013) and some others (Sanchez-Tojar, et al., 2018; Wang et al., 2018) for replicating studies in behavioral ecology, especially when relatively small sample sizes are used and studies are correlative.

**Dealing with spatiotemporal variation.** Based on long-term data from our study populations (Figure 3), it is difficult to determine if any of the five proxies estimating female blue tit coloration (blue and yellow brightness, blue hue, yellow and UV blue chroma) convey information about the [ability to lay a large clutch](#). We faced a similar problem when trying to interpret the results of a study on assortative mating and coloration in these same populations (Fargevieille, Grégoire, Charmantier, del Rey Granado, & Doutrelant, 2017). Based on data from around 1,600 pairs of birds, we observed highly variable patterns of assortative mating across space and time. These patterns fluctuated from positive to negative without ever being

clearly related to population, year, or coloration. We used a within-study meta-analysis (Nakagawa & Santos, 2012) to determine if there was a mean overall assortative mating pattern over the study period. We found that there was positive assortative mating based on UV-blue crown and yellow breast coloration and that the phenomenon varied in strength among the study populations. We used another within-study meta-analysis to determine whether female and male coloration traits were correlated with three life-history traits related to reproduction: laying date, clutch size, and fledging success. Although there was a high degree of spatiotemporal variation, overall, there were relationships between female **yellow and UV-blue** coloration and two maternal traits: laying date and clutch size. In addition, both **yellow and UV-blue** female and male coloration **were correlated** with fledging success (Fargevieille, Grégoire, Téplitsky, Del Rey & Doutrelant Unpublished). The next interesting step would be to explore the drivers of the inter-annual variability that we observed and to determine whether they **are due to** sampling error (Siepielski et al., 2013) and/or changes in environmental conditions, which may enhance, relax, or limit selection pressures on signals across time. It will be important to ascertain whether specific years and/or conditions have more of an influence than others. This task could be accomplished by examining variation in the opportunity for selection, which corresponds to the variance in fitness traits (Björklund & Gustafsson, 2013; Wade & Arnold, 1980). We have started looking at fluctuations in the opportunity for selection in our study populations (Figure 4), and there are clearly interesting patterns that merit further study.

**What do we know about male mate choice?** Above, we mentioned finding evidence of positive assortative mating based on UV-blue crown and yellow breast coloration (Fargevieille et al. 2017). This finding concurs with the results of (Hunt, Cuthill, Bennett, & Griffiths, 1999), who found that, in another population of blue tits, males displayed preferences associated with female UV-blue crown coloration. Furthermore, when we modified female and male yellow breast coloration, we found that it affected mutual mate choice, and that both **sexes**



preferentially select individuals with a pale chest plumage over colorful individuals (Caro, Doutrelant, Bonadonna et al. in prep). Consequently, sexual selection may be acting on both sexes in blue tits. Research in a Spanish blue tit population provided further support for this hypothesis when it found similar positive Bateman gradients for both females and males (García-Navas, et al., 2013). That said, similar research in a more northern blue tit population found positive opportunity for sexual selection in females but no positive Bateman gradient (Schlicht & Kempenaers, 2013). It may be that the differences in the results of these studies were due to random effects and/or differences in sample size/length of the studies. However, it is worth considering that southern populations face harsher breeding conditions than do northern populations because of lower food availability. As a result, it might be easier to detect selection pressures in southern populations. Only carrying out replicated studies across Europe will allow us to test this hypothesis. In addition, it appeared in both Garcia-Navas et al (2013) and Schlicht et al. (2013) that success with the social mate(s) contributed most to variation in male reproductive success, a result which could explain the interest for mate choice in this species.

**Female blue tit plumage coloration and female competition.** Blue tits breed in preexisting cavities, for which there is fierce competition (Kempenaers, 1994). We modified the hue of the female UV-blue crown to test if this trait could be used as a badge of status in female-female competition. In agreement with the prediction of the badge of status hypothesis, we found that females with a higher UV signal (i.e., a lower hue) reacted more aggressively to a decoy presenting a high UV signal (Midamegbe, Grégoire, Perret, & Doutrelant, 2011). To date, no other research of this type has been performed and the replicated studies conducted on this hypothesis on males show the importance of replicating this study (Alonso-Alvarez, et al., 2004; Korsten, et al., 2007; Rémy, et al., 2010; Vedder, et al., 2008). It is thus necessary to replicate

this experiment and to conduct complementary experiments to determine whether this behavior is due to competition for territories or mates.

(Table 4. about here)

**Evidence that blue tit plumage coloration is a condition-dependent signal.** Several studies have been conducted to determine if blue tit coloration can be condition dependent and why. Mild food restrictions during the molt did not affect UV-blue crown coloration (Peters, et al., 2011). By contrast coloration seem to be sensitive to change in the reproductive costs. We conducted experiments in which we forced both sexes to reproduce twice and later in the season and measured whether female and male coloration changed after the next molt. We found similar results for females and males: relative to individuals in the control group, individuals that were forced to invest in a second clutch late in the season displayed decreased UV-blue crown and yellow breast coloration (Doutrelant, et al., 2012). Mechanistically, this result could be explained by the treatment causing a reduction in molting time or an increase in stress levels at molt. Indeed, when the molt rate is experimentally increased, there is a decline in UV-blue crown reflectance, yellow breast brightness, and carotenoid chromaticity in both females and males (Ferns & Hinsley, 2008; Griggio, Serra, Licheri, Campomori, & Pilastro, 2009). Lastly, a link between condition and coloration is suggested by the negative relationship found between baseline corticosterone levels (when the nestling are five days old) and UV-blue crown chromaticity in female blue tits (Henderson, et al., 2013).

**Evidence that female blue tit coloration signals resistance to parasites.** As of yet, no clear pattern has been established between plumage coloration and parasitism. In a Spanish blue tit population, infection with avian malaria was negatively correlated with metrics of yellow breast coloration in both females and males – birds infected by multiple genera of parasites were paler (del Cerro et al., 2010). The opposite was true in a Swedish population - infected blue tits had higher levels of UV-blue crown coloration (greater brightness and UV chroma) and brighter

yellow breast plumage (Janas et al., 2018). Experimental work is thus necessary to explore this question in greater depth.

**Eggshell coloration—a potential female ornament in blue tits?** Eggshell coloration has been proposed to be a signal of quality used by the male to fine tune its investment in reproduction (Cherry & Gosler, 2010; Moreno & Osorno, 2003). Blue tit eggs have a white eggshell that is speckled with brown spots containing protoporphyrin-IX pigments (Kennedy & Vevers, 1976). We first investigated the potential for eggshell coloration to be a female ornament. Using both experiments and visual models, we found that blue tits could distinguish colors under dim light and thus in the dark of the cavity (Gomez et al., 2014; Holveck et al., 2010). We also established that mates and neighboring males visited nest cavities when eggs were present (Holveck, et al., 2010); a result also found in great tits (Firth, Verhelst, Crates, Garroway, & Sheldon, 2018). We then investigated whether eggshell coloration is related to egg and female quality. In our blue tit population, both correlative and experimental results suggest females of higher quality lay eggs with a larger brown-spotted surface area, more concentrated brown spots, higher white ground UV-chroma, and lower white ground brightness (Holveck, et al., 2012; Holveck, Guerreiro, Perret, Doutrelant, & Grégoire, 2019), a result that was found in another population (Badás et al., 2017; García-Navas et al., 2011; but not by: Martínez-de la Puente et al., 2007; Sanz & García-Navas, 2009). In another study, we modified eggshell coloration to determine whether it affected male investment: we found that it influenced male parental care, independently of female incubation or parental care patterns (Holveck, Doutrelant & Grégoire unpublished data). These results suggest that eggshell coloration could potentially function as a signal. This finding is also compatible with a more proximate hypothesis. Eggshell thickness is linked to reduced incubation time and higher hatching success in blue tits (García-Navas, et al., 2011; Sanz & García-Navas, 2009). It has been proposed that protoporphyrins have a structural function and could compensate for localized eggshell thinning (e.g., caused

by calcium deficiencies), thereby strengthening the eggshell and reducing permeability and water loss during incubation (Gosler, Higham, & Reynolds, 2005). This results so far got mixed experimental support in blue tits (García-Navas, et al., 2011; Holveck, et al., 2019). So overall, it seems that most findings are compatible with the fact that eggshell coloration in blue tits holds information on female and egg quality.

**Summary** - To conclude this section, we here specifically examined what the blue tit could tell us about the evolution of female coloration. The results of the research performed to date suggest that female coloration traits are condition-dependent and may function as sexual and social signals in this species. They also highlight the importance of carrying out (more) experimental studies as well as long-term studies. Indeed, the numerous studies we reviewed, with their similarities and differences, underscore that we need more research that will help clarify whether the differing conclusions could have arisen from spatiotemporal variation in environmental conditions and/or small sample sizes. Although this assessment may feel discouraging given the years of research on this subject, this is an important message for further studies and several research teams have made similar recommendations for other widely studied species, notably the house sparrow (*Passer domesticus*) and the zebra finch (Sanchez-Tojar, et al., 2018; Wang, et al., 2018).

## 7. General conclusions

Based on the collective results of the many studies mentioned in this review, female coloration appears to often function as a sexual ornament and/or a badge of status in birds. Our findings also suggest that, while female coloration might be sensitive to costs, it can still serve as a signal because there are many ways for females to use colors that do not result in trade-offs with fecundity.

In our review of the literature, we have identified some questions that still need more researches to be resolved and have call for specific changes in some of our research practices. Such changes could greatly improve our understanding of the forces driving the evolution of female ornaments. Below, we summarize our main points.

1. For research on macroevolution, we suggest that to advance farther, we need to leave behind the sexual dichromatism framework and its composite perspective, which conceal many evolutionary aspects of female (and male) coloration. Once freed, we can more accurately test the selective forces and constraints involved in the evolution of female coloration while simultaneously integrating information on the specific locations and coloration types of female ornaments. Adopting a female perspective and using female-specific indices of social and sexual selection to test hypotheses about the evolution of female coloration is particularly important. If this recommendation arose from our review of the comparative studies, it is important to note that it is applicable at both interspecific and intraspecific scales. The information in the signals targeted by male mate choice may differ from the information in the signals targeted by female mate choice. For instance, maternal effects and the maternal capacity to invest in eggs are female-specific characteristics, and research should include them in interspecific and intraspecific analyses whenever possible.

2. We need more studies to determine the strength of selection on the microevolution of coloration in different environments. This type of research requires long-term data, but many groups are already collecting such data for their study organisms. Indeed, we could establish consortia of researchers that are centered on given model systems. The greatest challenge is likely to be measuring sexual selection gradients because characterizing individual mating success is difficult in most wild bird populations. In particular, it is hard to sample unmated individuals, which leads to biased estimates and which is particularly an issue in long-term

monogamous species for which selection is on mate quality rather than mate quantity (Kvarnemo, 2018).

3. At the intraspecific level, we need to start performing studies where we compare female and male responses to the same experimental factors and where we modify several factors at the same time to compare for instance the effect of sexual and social contexts. Interestingly, a similar conclusion was recently reached for bird song. Riebel and colleagues (2019) argued that using such an approach could help eliminate biases: “the use of song for territorial defense is almost by default considered ‘sexually selected’ in males, but socially selected in females, whereas we cannot detect obvious contextual differences in many cases”(Riebel, et al., 2019).

4. Lastly, using our study model, the blue tit, we underscored the need to conduct replicated studies and complementary studies. Such studies should focus on a single study system, with a view to distinguishing statistical artefacts from robust patterns. Also, we pointed the interest of employing long-term studies and appropriate statistical tools (e.g., within-study meta-analyses) to contrast estimates obtained between years or sites and to compare short- versus medium-term microevolutionary trajectories. These recommendations should be applicable to all the species studied so far, and researchers have arrived at similar conclusions for other well-studied species models (Sanchez-Tojar, et al., 2018) and for male blue tit coloration (Parker, 2013). They are also applicable to any species given that sexual and social traits are highly sensitive to environmental conditions, population densities, local sex ratios, and neighborhood characteristics (Cornwallis & Uller, 2010).

Before concluding, we wish to mention two final perspectives that were not explored in this review but that appear important to tackle. First, using a multimodal approach to study female traits (i.e., sexually and non-sexually selected traits) can expand our understanding of their evolution. At least four different families of sexually selected traits have been described in female birds: song, body coloration, behavioral displays, and egg coloration. Some studies are

starting to include both female song and coloration in their analyses (Gomes, Funghi, Soma, Sorenson, & Cardoso, 2017; Hasegawa, Arai, Watanabe, & Nakamura, 2017; Soma & Garamszegi, 2018; Webb et al., 2016). Second, sexual selection is presented as being intrinsically linked to individual success and the adaptability of populations. This perspective is rooted in the notion of good genes, in which selection is directed against deleterious mutations (Agrawal, 2001; Siller, 2001; Whitlock, 2000). It arose from the results of theoretical studies in which sex roles were assumed to be extremely conventional: in the models, males displayed and females chose. In this framework, many males are purged via sexual selection, allowing the population to rid itself of deleterious mutations without paying the full demographic price. However, if females are also sexually selected, it is uncertain how [the](#) model output would change.

In closing, we hope this review has provided solid groundwork for future research on the vast subject of female ornaments.

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## Box 1: Quantifying coloration

Bird coloration was one of the first ornaments to be used to test hypotheses about sexual selection and ornament evolution, mainly because so much of the variation in bird coloration can be easily seen by humans. In the beginning, coloration traits were scored using the human eye, reference specimens, and reference color plates; studies made distinctions between “drab” and “bright” colorations (Badyaev, 1997; Hamilton & Zuk, 1982) and similar versus different colorations (Irwin, 1994). Such methods are still common today (Dale, et al., 2015; McQueen et al., 2019; Negro, et al., 2018; Juan José Soler, et al., 2019; Webb, et al., 2016). However, the use of far more precise tools, namely spectrophotometry, has revealed something that is invisible to the human eye: in many species, there is variation in the ultraviolet (UV) part of the signal emitted by coloration traits. Neurophysiologists discovered that birds have four types of photoreceptors, including one that is sensitive to UV or violet radiation, depending on the species (Bennett & Cuthill, 1994). In contrast, humans have just three types of photoreceptors, and none of them can detect UV radiation. Furthermore, there are oil droplets on the bird retina that change cone sensitivity (Hart & Vorobyev, 2005). To analysis coloration, it is therefore important not only to take advantage of high-precision tools (e.g., spectrophotometry and calibrated cameras with UV filters), but also to account for other factors that can modify color perception, such as light conditions, background, and the visual abilities of the receiver (Endler, Westcott, Madden, & Robson, 2005), which can be done using [multiple](#) software (Gomez, 2010 ; Maia, Gruson, Endler, & White, 2019; Stoddard & Prum, 2011)

Even though several studies have found some degree of correlation between human vision and characterizations of bird vision (Armenta, Dunn, & Whittingham, 2008; Bergeron & Fuller, 2018; Dale, et al., 2015; Seddon, Tobias, Eaton, & Odeen, 2010), it seems important that we should strive to properly assess true variation in coloration traits, rather than simply relying on assessments using human vision (Stoddard, Miller, Eyster, & Akkaynak, 2018). For instance,

the overlap in photoreceptor sensitivity is different between birds and humans—birds and humans likely distinguish colors differently, which may result in differences in perception (Håstad & Ödeen, 2008). Indeed, Eaton (2005) found that more than 90% of the species classified as monochromatic based on human vision were actually dichromatic based on spectrophotometry (and: Armenta, et al., 2008; see also: Kevin J Burns & Shultz, 2012; Eaton, 2005). It therefore seems especially important to take advantage of quantitative tools when addressing questions related to intraspecific communication, especially when human vision may fail to pick up on subtle but essential variation in coloration (Bergeron and Fuller 2018).

## Box 2: The limits of the sexual dichromatism framework

Sexual dichromatism can be defined as the existence of differences in coloration between males and females of the same species. In contrast, sexual monochromatism describes the situation in which males and females show no differences in coloration. Variation in sexual dichromatism is often used as a proxy for the intensity of sexual selection (e.g., Cooney et al. 2019 for a very recent reference) and to test hypotheses related to the evolution of coloration traits (Dustin R Rubenstein, 2012; Simpson, Johnson, & Murphy, 2015; Juan José Soler, et al., 2019). However, the terms *dichromatism* and *monochromatism* conceal a broad range of coloration scenarios. Species classified as sexually monochromatic can be fully drab, drab with small patches of color, slightly colored, or very conspicuous. Similarly, in dichromatic species, it is not necessarily the case that one sex is highly conspicuous, while the other is drab (Figure 1). In some species, both males and females can be conspicuous, but males may bear a contrasting and highly conspicuous patch that is absent from females. Some dichromatic species can also be “drab,” with the sexes differing in their display of brown coloration (Marcondes & Brumfield, 2019). Additionally, sexual dichromatism is currently understood to be a composite trait that reflects different evolutionary forces acting independently on males and females (Dale, et al., 2015; Irwin, 1994; J. J. Price & Eaton, 2014). For these two reasons, using sexual

dichromatism as a proxy for the intensity of sexual selection should not be done automatically.

Of course, when examining the evolution of plumage coloration, it is possible to test the association between sexual dichromatism and various factors, but the analysis should be coupled with separate analyses focused specifically on female and male coloration traits in order to tease apart the numerous forces shaping sexual dichromatism (Dale et al. 2015, Dunn et al. 2015, Cooney et al. 2019).

## Tables

**Table 1.** Comparative studies exploring the factors involved in the evolution of female coloration in birds

<b>Family/C lade</b>	<b>Research focus</b>	<b>Proxy for sexual selection</b>	<b>Other proxies</b>	<b>Color assessment method</b>	<b>Body parts examined</b>	<b>Genetic correlati on</b>	<b>Separ ate tests for female and male colora tion?</b>	<b>Sexual dichromatis m present</b>	<b>Association with female coloration</b>	<b>Reference</b>
African Sturnidae (45 species)	Is monochromatism more common in species where female access to reproduction is limited?	Cooperative breeding (intrasexual selection)		Human vision used to score degree of monochromatis m/dichromatis m	Whole body	Not applicable	No	Yes	Sexual monochromatism is associated with female social selection	Rubenstein & Lovette 2009
Songbirds (~6000 species)	Role of sexual and natural selection in shaping female and male plumage coloration	Social mating system, sexual size dimorphism, paternal care	Breedin g latitude, clutch size, seasonal ity, migratio n	RGB from scanned reference plates	Nape, crown, forehead, throat, upper breast, lower breast	Yes	Yes	Yes, but also differences in male and female plumage	Positive relationship between female body size and tropical life traits. Negative relationship between migration and sexual selection.	Dale et al. 2015



No specific clade (~977 species)	Role of sexual and natural selection in sexual dichromatism and monochromatism/Evolutionary shifts between sexual monochromatism and dichromatism	Social mating system, testes size (body mass)	Body mass, breeding latitude, habitat cover, migratory behavior, development (precocial to altricial), nest height, cavity nesting, paternal care (absence/presence)	Spectrophotometry values converted into principal components	Crown, back, tail, throat, belly, wing coverts	Not mentioned	Yes	Yes, but as a continuous (or semi-discrete) variable	Transition to monochromatism equally associated with female plumage and male plumage.	Dunn et al. 2015
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Australian landbirds (555 species)	Color gamut of female and male plumage	Not applicable	Not applicable	Spectrophotometry values and avian visual space analysis	Front, crown, dorsal neck, upper back, lower back, rump, tail proximal, tail distal, wing primaries, vent, wing coverts, belly, lower breast, upper breast, ventral neck, throat, cheek	Not applicable	Yes	Not estimated	Female gamut smaller than male gamut	Delhey 2015
Maluridae (15 species)	Relationship between habitat structure and female and male plumage	Not applicable	Habitat structure (PCA)	Constraints estimated from spectrophotometry values and avian visual space analysis	Head, back, breast, belly, cheek, throat, tail	Not mentioned	Yes	Not estimated	Negative relationship with habitat openness	Medina et al. 2017
Thraupidae (351 species)	Role of sexual and natural selection in shaping patterns of sexual dichromatism	Sexual dichromatism	Habitat (open/closed), foraging stratum, subfamily	Spectrophotometry values + avian color space analysis converted into principal components	Crown, back, rump, dorsal tail, crissum, belly, breast, throat, primaries	Not mentioned	Yes	Yes (tested against the principal components for female and male plumage )	Sexual dichromatism of the dorsal tail best fits a female coloration model (non-statistically significant trend also seen in wing	Shultz & Burns 2017

									primaries and tail)	
Western Palearctic avifauna (666 species)	Relationship between melanin-based sexual dichromatism and female and male plumage coloration	Not applicable	Not applicable	Human vision used to assign scores based on reference plates	Bill, crown-nape, chin-eye, breast, belly, legs, back-tail-folded wings	Not applicable	No	Yes	More species with light females and dark males than expected by chance	Negro et al. 2018
Tyrannidae, Pipridae, Cotingidae (372 species)	Rate and direction of (interspecific) divergence in coloration	Sexual dichromatism	Time since divergence, body mass, dependence on forest habitat, latitude, confamilial sympatry	Photos converted to RGB + avian color space	Crown, nape, mantle, rump, tail, wing coverts, wing primaries, throat, breast, belly	Correlation between sexes in the rate of divergence	Yes	Yes, as a proxy for the intensity of sexual selection	Rates of female plumage divergence not associated with dichromatism	Cooney et al. 2019

Songbirds (178 species)	Relationship between male nest-building behavior and female conspicuousness	No details provided about the indices tested (whether for natural or sexual selection)	Nest type, female body mass, male and female contribution to nest building	Human vision used to score conspicuousness based on reference plates	Whole body	Not mentioned	No	Yes, as the dependent variable	Female conspicuousness positively associated with male contribution to nest-building	Soler et al. 2019
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**Table 2.** Species for which Opportunity for selection, opportunity for sexual selection and/or Bateman gradient have been calculated for females and males.  $dI_{\lnCVR}$  is the effect size for sex difference in opportunity for selection,  $dI_{\lnCVR\_VAR}$  is the variance of  $dI_{\lnCVR}$ ,  $dIs_{\lnCVR}$  is the effect size for sex difference in opportunity for sexual selection,  $dIs_{\lnCVR\_VAR}$  is the variance of  $dIs_{\lnCVR}$ ,  $dbeta\_g$  is the effect size for sex difference in Bateman gradient,  $dbeta\_g\_VAR$  is the variance of  $dbeta\_g$ ,  $f\_beta\_z$  is the female Bateman gradient,  $f\_beta\_z\_VAR$  is the variance of  $f\_beta\_z$ . Data issued from Janicke et al. 2016. Positive value for the 3 metric estimating sex difference indicate that metrics are male biased (the larger the value, the stronger is the male bias, negative values indicate a female bias). Positive value for  $f\_beta\_z$  indicates an association between mating success and reproductive success in females.

Species	Authors	Year	Journal	Parental care	Dimorphism	$dI_{\lnCVR}$	$dI_{\lnCVR\_VAR}$	$dIs_{\lnCVR}$	$dIs_{\lnCVR\_VAR}$	$dbeta\_g$	$dbeta\_g\_VAR$	$f\_beta\_z$	$f\_beta\_z\_VAR$
Cyanistes_caeruleus	Garcia-Navas et al,	2014	Behav Ecol	shared	male-biased					0.05	0.03	0.36	0.02
Cyanistes_caeruleus	Schlicht & Kempenaers	2013	Evolution	shared	male-biased	0.34	0.0003	0.15	0.0004	0.45	0.0002	0.0002	0.0002
Delichon_urbica	Whittingham & Lifjeld	1995	J Avian Biol	shared	male-biased	0.53	0.15	0.00	0.15	0.60	0.21	-0.07	0.13
Delichon_urbica	Whittingham & Lifjeld	1995	J Avian Biol	shared	male-biased	0.96	0.14	0.58	0.14	1.01	0.19	0.16	0.17
Dendroica_pensylvanica	Byers et al,	2004	Auk	shared	male-biased	0.66	0.05	0.39	0.06	0.95	0.06	0.57	0.03
Gallus_gallus	Collet et al,	2012	PNAS	only female	male-biased	0.31	0.07	0.72	0.04	0.46	0.15	0.68	0.10
Geothlypis_trichas	Whittingham & Dunn	2005	Behav Ecol	shared	male-biased	0.57	0.08			0.50	0.10	0.31	0.06
Jacana_jacana	Emlen & Wrege	2004	The Auk	only male	female-biased			-0.24	0.01				
Junco_hyemalis	Gerlach et al,	2012	Behav Ecol	shared	male-biased	0.19	0.01	0.17	0.0003	0.74	0.0004	0.31	0.0002
Junco_hyemalis	Ketterson et al,	1997	Ornithol Monogr	shared	male-biased	0.17	0.05	0.27	0.04	-0.12	0.04	1.01	0.02
Meleagris_gallopavo	Krakauer	2008	Condor	only female	male-biased	0.63	0.07	0.44	0.05	0.65	0.07	0.34	0.04
Molothrus_ater	Woolfenden et al,	2002	Behav Ecol Sociobiol	none	male-biased	0,23	0,03	0,30	0,02	-0,02	0,01	0,86	0,01
Notiomystis_cincta	Walker et al,	2014	J Evol Biol	shared	male-biased	0,41	0,03	0,60	0,02	0,12	0,02	0,46	0,01

Sialia_currucoides	Balenger et al.	2009	J Avian Biol	shared	male-biased	1.01	0.02	0.35	0.02	0.84	0.04	0.06	0.02
Zonotrichia_leucophrys	Poesel et al.	2011	Auk	shared	male-biased	0.78	0.03	-0.28	0.03	0.68	0.04	0.19	0.02

**Table 3.** The 16 bird species in which the badge-of-status hypothesis has been tested experimentally

Species	Color	Coloration type	Color and/or size	Location	Type of experiment	Support for hypothesis?	References
Northern cardinal ( <i>Cardinalis cardinalis</i> )	Black	Melanin	Color & size Size	Mask	Decoy Decoy	Yes No	Jawor, et al., 2004 Winters & Jawor, 2016
North American barn swallow ( <i>Hirundo rustica erythrogaster</i> )	Black	Melanin	Color	Ventral area	Plumage modification	Yes	Vitousek, et al., 2013
Common kestrel ( <i>Falco tinnunculus</i> )	Gray or brown	Melanin	Presence	Rump	Decoy	Yes	Lopez-Idiaquez, Vergara, Fargallo, & Martínez-Padilla, 2016
Streak-backed oriole ( <i>Icterus pustulatus pustulatus</i> )	Orange	Carotenoid	Color	Breast	Decoy	Yes	Troy G Murphy, Rosenthal, Montgomerie, & Tarvin, 2009
American goldfinch ( <i>Spinus tristis</i> )	Yellow	Carotenoid	Color	Bill	Decoy	Yes	Troy G. Murphy, Hernandez-Mucino, Osorio-Beristain, Montgomerie, & Omland, 2009
	Yellow	Carotenoid	Color	Bill	Wing clipping and social experiment	Yes	
Rock sparrow ( <i>Petronia petronia</i> )	Yellow	Carotenoid	Size	Breast	Food competition	Yes	Zanollo, et al., 2013
Prothonotary warbler ( <i>Protonotaria citrea</i> )	Yellow	Carotenoid	Color	Breast	Breeding site	Partially	Beck, 2013
Common waxbill ( <i>Estrilda astrild</i> )	Red	Carotenoid	Color	Bill	Stimulation of testosterone secretion via GnRH challenge	No	Funghi, et al., 2018
Crimson finch ( <i>Neochmia phaeton</i> )	Red	Carotenoid	Color	Chest spottiness	Mount	Partially	Young, Cain, Svedin, Backwell, & Pryke, 2017

European starling ( <i>Sturnus vulgaris</i> )	White	Structural	Number	Chest spottiness	Plumage modification	Yes	Swaddle & Witter, 1995
Collared flycatcher ( <i>Ficedula albicollis</i> )	White	Structural	Size	Wing patch	Decoy	Yes	Hegy, Garamszegi, Eens, & Török, 2008
Pied flycatcher ( <i>Ficedula hypoleuca</i> )	White	Structural	Size	Wing patch	Size	Yes	Plaza, et al., 2018
			Size	Forehead patch	Decoy	Yes	Morales et al., 2014
Diamond firetail ( <i>Stagonopleura guttata</i> )	White	Structural	Number	Flank spots	Feeding trials/food contests	Yes	Crowhurst, Zanollo, Griggio, Robertson, & Kleindorfer, 2012
Blue tit ( <i>Cyanistes caeruleus</i> )	UV-blue	Structural	Color	Head	Decoy	Yes	Midamegbe, et al., 2013
Lovely fairywren ( <i>Malurus amabilis</i> )	Blue	Structural	Color	Cheek	Mirror & Color	Yes	Leitão, et al., 2019
Tree swallow ( <i>Tachycineta bicolor</i> )	Iridescent blue-green	Structural	Color	Back	Brightness modification	Yes	Berzins & Dawson, 2018
					Decoy	No for green-blue; Yes for white	



**Table 4.** Studies that examined whether female blue tit coloration was subject to social or sexual selection (the publications are ordered by main theme and year)

<b>Research focus</b>	<b>Main theme and presence of evidence (Yes/No)</b>	<b>Result</b>	<b>Experimental study?</b>	<b>Number of individuals</b>	<b>Number of years</b>	<b>Location of study population</b>	<b>Authors</b>
Relationship between UV-blue crown coloration and female and male mate choice	Mutual choice: Yes	UV-blue crown coloration is important in female and male mate choice	Yes	24 (50% females)	1	UK	Hunt et al. 1999
Relationship between UV-blue crown coloration and resource allocation	Male choice: Yes	Males provide more food to the nestlings of more colorful females	Yes (UV-blue crown coloration reduced)	30 males (and 30 modified females)		Austria	Mahr et al. 2012
Relationship between UV-blue crown coloration and resource allocation	Male choice: No	Males provide less food to the nestlings of less colorful females; females provide more food to the nestlings of more colorful males	No	33 females and 33 males	1	Netherlands	Limbourg et al. 2013
Relationship between UV-blue crown coloration and resource allocation	Male choice: No	Males provide less food to the nestlings of less colorful females; females provide more food to the nestlings of more colorful males	Yes (UV-blue crown coloration reduced)	Not found	1	Netherlands	Limbourg et al. 2013
Association between UV-blue crown and yellow breast coloration and assortative mating	Mutual Choice: Yes	Assortative mating based on UV-blue crown and yellow breast coloration	No	~1200 (about 50% females)	10	France	Fargevieille et al. 2017
Relationship between UV-blue crown and yellow breast coloration and competition in females	Social selection: Yes	Females with a higher UV signal (i.e., lower hue) were more aggressive towards UV-enhanced intruders; females with a lower UV signal (i.e., higher hue) were more aggressive towards UV-reduced intruders; females with darker yellow chests were more aggressive towards intruders	Yes (decoys with reduced vs. enhanced UV)	48 females	1	France	Midamegbe et al. 2011

(1) Heritability & (2) Link with offspring recruitment and size	(1) Heritability: Yes; (2) Parental quality: No	(1) Low/no heritability of either trait; (2) No link with offspring fitness	Yes (cross-fostering)	(1) 368; (2) 283	3	UK	Hadfield et al. 2006
(1) Heritability & (2) Genetic correlation	(1) Heritability: small amount of support; (2) Genetic correlation: Yes	(1) Low heritability for both traits; (2) Strong genetic correlation for UV-blue coloration	No	More than 3000	9	France	Charmantier et al. 2017
Relationship between UV-blue crown, yellow breast coloration and maternal quality	Maternal quality: Yes	Intensity of UV-blue crown coloration is positively correlated with egg size in female blue tits	No	28 (50% females)	1	Hungary	Szigeti et al. 2007
Fecundity-based selection on female and male UV-blue crown and yellow breast coloration	Maternal quality: Yes	Brighter yellow females produced more eggs and tended to recruit more offspring, but only in the experimental group; yellower females (higher yellow chroma) fledged more chicks; there was no effect of male coloration	Yes (clutch removal)	~140 (50% females)	1	France	Doutrelant et al. 2008
Fecundity-based selection on female and male UV-blue crown and yellow breast coloration	Maternal quality: No	Selection strength was variable but largely weak and disruptive in nature; it was disruptive for yearling females chest and males crest colour. In adult females, it was a marginally nonsignificant positive linear selection on crown plumage colour.	No	~600 (about 50% females)	3	UK	Parker et al. 2011

Relationship between yellow breast coloration and parental care	Maternal quality: Yes	Female and male yellow chroma is linked to parental care (positively with nestling provisioning rates and proportion of Lepidoptera larvae brought to the nest for both males and females), but only female, but not male, yellow coloration is positively linked to breeding success (proportion of fledged young).	No	~70 (about 50% females)	2	Spain	Garcia-Navas et al. 2012
Relationship between UV-blue crown coloration and female quality	Maternal quality: Yes	Negative association between female UV-blue crown coloration and corticosterone when nestlings are 5 days old, positive association between crown coloration and fledgling number	No	84 females for corticosterone; 103 females for fledgling success	3	UK	Henderson et al. 2013
Relationship between female coloration and female quality	Maternal quality: Yes	Brighter yellow females put more carotenoids into their eggs but only in the vaccinated group	Yes (vaccination)	45 females	1	France	Midamegbe et al. 2013
Relationship between UV-blue crown and yellow breast coloration and parental investment	Maternal quality: No	No links with female and male coloration (except maternal carotenoid based coloration which positively relate to offspring begging)	No	~103 (about 50% females)	2	Belgium	Lucass et al. 2016
Effect of (1) habitat quality and (2) molt rate on yellow breast coloration	Condition dependence: Yes	(1) No effect of habitat; (2) Effect of molt rate on yellow saturation in females	(1) No for habitat quality; (2)	(1) 247 males and females; (2) 10 females	(1) 6 years;	UK	Ferns & Hinsley 2008

		(decreased chroma when molt is faster)	Yes for molt rate		(2) 1 year		
Effect of molt rate on UV-blue crown, yellow breast, and white coloration	Condition dependence: Yes	Increasing the molt rate by rapidly decreasing the photoperiod decreased UV-blue crown coloration levels and yellow breast brightness (but did not change white coloration)	Yes (molt rate)	12 females, 14 males	1	Italy	Griggio et al. 2009
Effect of hemosporidian infection status on UV-blue crown and yellow breast coloration	Condition dependence: Yes	Multiple infections had negative influence on carotenoid-based coloration (same effect on both sexes, data on parasitism and coloration collected at the same time [during rearing])	No	166 (about 50% females)	3	Spain	del Cerro et al. 2010
Condition dependance of UV-blue and white coloration traits	Condition dependence: No	No effect of food restriction on UV-blue crown or white coloration in either females and males	Yes (food restriction)	48 individuals	1	Germany	Peters et al. 2011
Condition dependance of UV-blue crown and yellow breast coloration	Condition dependence: Yes	Control birds (females and males) showed a greater increase in UV-blue crown and yellow breast coloration with age than did experimental birds; treatment effect was smaller for higher quality females	Yes (clutch removal)	85 (about 50% females)	4	France	Doutrelant et al. 2012

Effect of hemosporidian infection status on UV-blue crown and yellow breast coloration	Condition dependence: No	Infected blue tits had higher levels of UV-blue crown coloration (greater brightness and UV chroma) and brighter yellow breast plumage (same effect in both sexes, data on parasitism and coloration collected at the same time [during rearing])	No	492 individuals (about 50% females)	3	Sweden	Janas et al. 2018
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## Figures captions

**Figure 1.** Examples of sexual dichromatism and monochromatism. The golden-headed manakin (*Ceratopipra erythrocephala*) provides an example of conventional dichromatism: the male (a) is highly conspicuous and displays contrasting colors, while the female (b) is cryptic. The northern slaty antshrike (*Thamnophilus punctatus*) provides an example of less dramatic dichromatism: the male (c) has gray coloration and the female (d) has brown coloration. The sociable weaver (*Philetarius socius*) provides an example of conventional monochromatism: both the male (e) and female (f) are drab but have melanin based patches. The Martinique oriole (*Icterus bonana*) provides an example of mitigated monochromatism: the male (g) and female (h) have similar black and rusty coloration. The blue tit (*Cyanistes caeruleus*) provides an example of conspicuous monochromatism: the male (i) and female (j) have similar conspicuous blue and yellow coloration. It should be noted here that the blue tit displays cryptic dichromatism in the UV reflectance of its blue crown that is invisible to the human eye. Photos: Franck Théron (a–d, g, and h), Elise Blatti (e and f), and Claire Doutrelant (i and j).

**Figure 2. A)** Locations of the four populations that our research group in Montpellier (Southern France) study to determine the role of selection and genetic constraints in the evolution of female and male ornaments in blue tits. **B)** A female blue tit incubating her eggs. **C)** Blue tit hatchlings **D)** Nestlings nearly ready to fledge. Our team mostly works on two plumage ornaments: the UV-blue crown and the yellow breast patch. Our goal is to simultaneously analyze data from females and males. Since 2005, we have collected feathers from both ornaments to characterize the coloration traits of every blue tit (around 800 sexually mature individuals/year) that is breeding in the nest boxes in our four study populations. Photos: Claire Doutrelant.

**Figure 3.** Estimates of directional selection gradient relating clutch size in relation to female blue tit plumage coloration in our four studied populations from 2005 to 2014. Two variables of coloration (brightness and chromaticity) were quantified for two patches (UV-blue crown and yellow breast patches). Error bars illustrate associated standard deviation. Grey dotted lines illustrate a null gradient of selection (0). Color variables are not available for the two Muro populations in 2007.

**Figure 4.** Variation in the opportunity for selection from 2005 and 2014, in our four blue tit studied populations. For each year in each population, variables of interest (clutch size and fledging success) were centered to a mean of 1. Opportunity for selection was then estimated as the variance associated to these centered variables.