



REVIEW

Plumage patterns: Ecological functions, evolutionary origins, and advances in quantification

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ABSTRACT

Birds exhibit remarkable variation in plumage patterns, both within individual feathers and among plumage patches. Differences in the size, shape, and location of pigments and structural colors comprise important visual signals involved in mate choice, social signaling, camouflage, and many other functions. While ornithologists have studied plumage patterns for centuries, recent technological advances in digital image acquisition and processing have transformed pattern quantification methods, enabling comprehensive, detailed datasets of pattern phenotypes that were heretofore inaccessible. In this review, we synthesize recent and classic studies of plumage patterns at different evolutionary and organismal scales and discuss the various roles that plumage patterns play in avian biology. We dissect the role of plumage patches as signals within and among species. We also consider the evolutionary history of plumage patterns, including phylogenetic comparative studies and evolutionary developmental research of the genetic architecture underlying plumage patterns. We also survey an expanding toolbox of new methods that characterize and quantify the size, shape, and distribution of plumage patches. Finally, we provide a worked example to illustrate a potential workflow with dorsal plumage patterns among subspecies of the Horned Lark (*Eremophila alpestris*) in western North America. Studies of plumage patterning and coloration have played a prominent role in ornithology thus far, and recent methodological and conceptual advances have opened new avenues of research on the ecological functions and evolutionary origins of plumage patterns in birds.

Keywords: coloration, digital photography, image processing, patterning, patterns, plumage

LAY SUMMARY

- Birds have many different plumage patterns that arise from coloration motifs within feathers as well as differences in color among body regions.
- Plumage patterns play various roles in bird biology. They are involved in mate choice and territoriality, social interactions, camouflage from predators, and many other functions.
- There is a rich history of detailed study on plumage patterns, which we review and synthesize in this manuscript.
- Recent advances in photography and image processing algorithms have opened new avenues of research on plumage patterns. These open-source methods enable efficient, repeatable, and scalable analytical pipelines.
- We illustrate one possible pipeline with a worked example of geographic variation in dorsal plumage patterns among populations of Horned Lark (*Eremophila alpestris*) in the western United States.
- Looking ahead, enhanced capacity and scalability for digital photography analyses will reveal new discoveries regarding the ecology and evolution of avian plumage patterns.

Patrones de plumaje: funciones ecológicas, orígenes evolutivos y avances en cuantificación

RESUMEN

Las aves exhiben variación muy marcada en los patrones de plumaje, tanto dentro de plumas individuales como entre parches de plumaje. Las diferencias en tamaño, forma y ubicación de los pigmentos y de los colores estructurales abarcan señales visuales importantes involucradas en la selección de pareja, el señalamiento social, el camuflaje y muchas otras funciones. Aunque los ornitólogos han estudiado los patrones de plumaje durante siglos, los avances tecnológicos recientes en la obtención y procesamiento de imágenes digitales han transformado los métodos de cuantificación de los patrones, permitiendo bases de datos detalladas y completas de fenotipos de patrones que fueron hasta ahora inaccesibles. En esta revisión, sintetizamos estudios recientes y clásicos de los patrones de plumaje a diferentes escalas evolutivas y de organismos y discutimos los múltiples roles que los patrones de plumaje juegan en la biología de las aves.

Analizamos el rol de los parches de plumaje como señales dentro y entre especies. También consideramos la historia evolutiva de los patrones de plumaje, incluyendo estudios filogenéticos comparativos y la investigación evolutiva del desarrollo de la arquitectura genética que subyace a los patrones de plumaje. Estudiamos además las herramientas en expansión de nuevos métodos que caracterizan y cuantifican el tamaño, la forma y la distribución de los parches de plumaje. Finalmente, brindamos un ejemplo para ilustrar un flujo de trabajo potencial con patrones de plumaje dorsal entre subespecies de *Eremophila alpestris* en el oeste de Norteamérica. Los estudios de los patrones y de la coloración del plumaje han jugado un rol predominante en la ornitología hasta ahora, y los avances metodológicos y conceptuales recientes han abierto nuevas líneas de investigación en la ecología y los orígenes evolutivos del patrón de plumaje en las aves.

Palabras clave: coloración, fotografía digital, patrones, plumaje, procesamiento de imágenes

INTRODUCTION

Bars, bibs, badges, chevrons, spots, scales, streaks, stripes, and plumage patches of all shapes and sizes play important roles in avian biology (Figure 1). Plumage patterns are targets of sexual selection (Price 1998), serve as social cues among individuals (Santos et al. 2011), and provide camouflage against visual predators (Stevens and Merilaita 2011), among many other functions (Burt 1981, Hill and McGraw 2006, Cuthill et al. 2017, Pérez-Rodríguez et al. 2017).

Plumage patterns arise when pigments or structural colors are non-uniformly distributed on an organism's body. They vary among species, but also differ among ontogenetic developmental stages, sexes, physiological conditions, social statuses, and phenological seasons within species (Price and Pavelka 1996, Galeotti et al. 2003). Patterning in birds occurs at multiple scales: coordinated and localized patterns of within-feather color variation can generate repeated patterns or motifs in a localized area (Prum and Williamson 2002), while coloration differences among feather tracts of various body patches create broader-scale patterning across an organism's body (Stoddard and Prum 2008). Because plumage patches are readily observable and serve various important roles in avian biology, they have been studied extensively by ornithologists. Classic works by Darwin (1871), Wallace (1877), Thayer (1896, 1909), and Cott (1940) have inspired generations of naturalists to investigate the biological function and evolutionary origins of avian patterning and coloration (Butcher and Rohwer 1989, Savalli 1995, Hill and McGraw 2006).

Building upon the foundation of hundreds of individual studies, recent advances in digital image acquisition and processing have opened new avenues of research on animal coloration patterns (Stoddard and Osorio 2019). Computer vision, which collectively describes modern methods of digital image acquisition and processing, relies on individual and aggregate pixel values to infer image content (Weinstein 2018), whereas “machine-learning” or “deep-learning” enables us to efficiently and accurately quantify and categorize the information stored in images (Christin et al. 2019, Miao et al. 2019). This expanding toolbox holds great promise to facilitate exciting discoveries into

longstanding questions and new avenues of research in ornithology and biology more generally (McKay 2013, Pérez-Rodríguez et al. 2017).

In this review, we synthesize insights from recent and classic studies of avian plumage patterns. Specifically, we discuss how plumage patterns function as targets of sexual selection and social signals among members of the same species, but also review how plumage patterns contribute to ecological and evolutionary dynamics among species. We summarize recent discoveries regarding the evolutionary origin of plumage patterns achieved through phylogenetic comparative studies, and consider how high-throughput sequencing has shed light on the genetic architecture and evolutionary development of plumage patterns. Finally, we summarize recently developed methods that quantify plumage patterns, discuss their various strengths and limitations, and illustrate a potential analytical pipeline by quantifying dorsal pattern variation among subspecies of the Horned Lark (*Eremophila alpestris*).

The language of animal coloration patterns is sometimes confusing and inconsistent. While coloration and patterning are closely linked and are often used interchangeably, we make a distinction in this review and focus primarily on avian patches, patterns, and patterning. In an attempt to clarify the language used here, we define coloration as the hue, chroma, or brightness of an individual feather or group of feathers that comprise a single, continuous plumage patch. We consider patches as body regions with uniform coloration (i.e. share the same hue, brightness, and chroma). Occasionally, there may be gradual change in some aspect of coloration within a single patch (e.g., the diffuse red “bib” of some male House Finches [*Haemorrhous mexicanus*]), but patches generally contrast strongly with adjacent or background colors. We define patterning as the broader spatial arrangement of body regions or feather tracts that differ in some aspect of their coloration, whereas patterns refer to repeated “motifs”—such as bars or spots—within or among feathers of a body region. Occasionally, patterns may also refer to broader spatial arrangements of colors or individual patterns among body parts, but we consider “patterning” a broader spatial term that can encompass various “patterns” among body regions. Thus, while coloration and patterning are

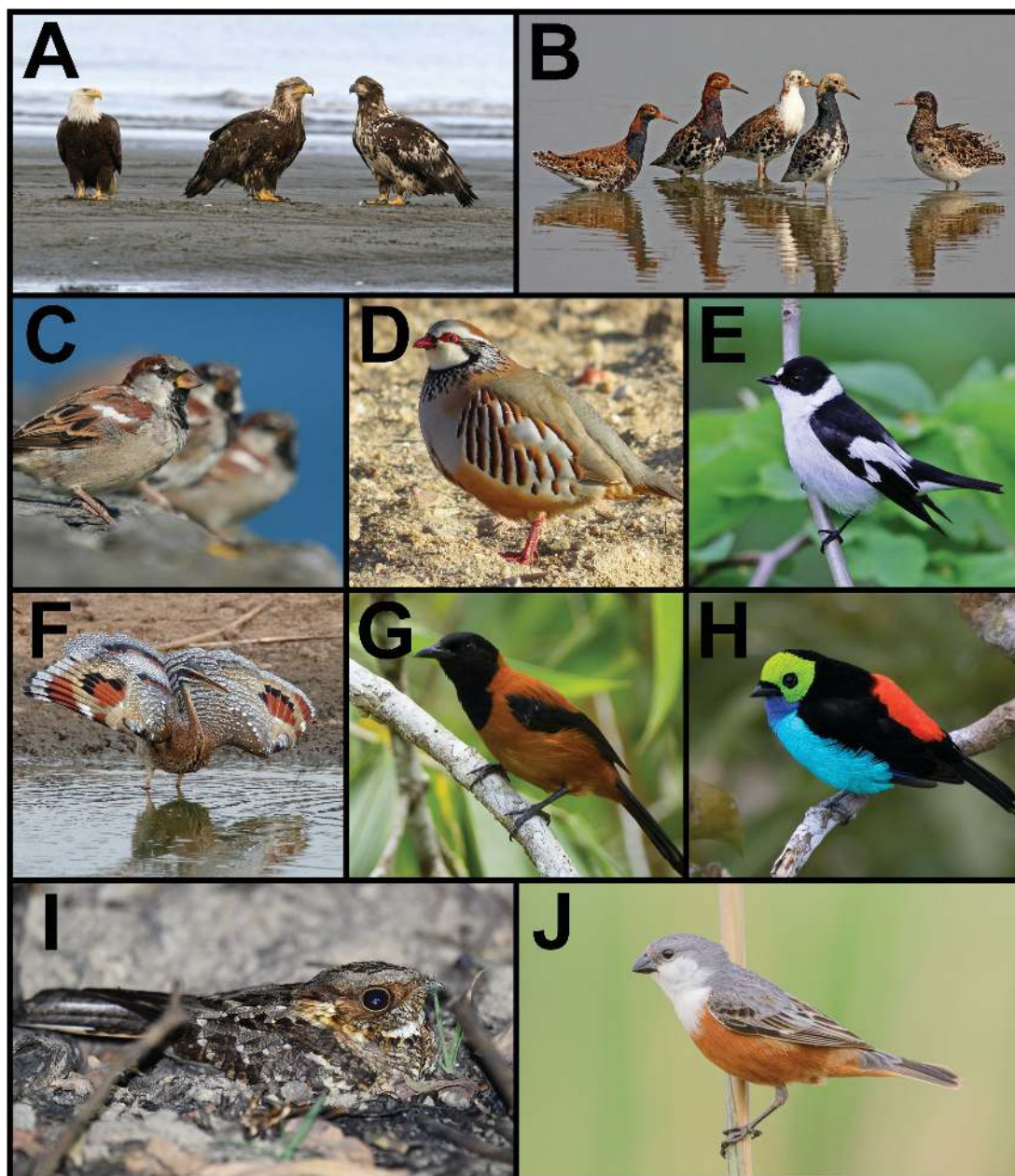


FIGURE 1. Diversity of plumage patterns in birds and their roles in avian biology highlighted in this review. **(A)** Bald Eagles (*Haliaeetus leucocephalus*) exhibit ontogenetic differences in plumage patterns between age classes (photo credit: Lars Petersson; Macaulay Library Catalog Number 205975811). **(B)** Ruffs (*Philomachus pugnax*) use plumage patterns to identify individuals and alternate patterns are associated with different male breeding strategies (photo credit: Frans Vandewalle; ML205648651). **(C)** House Sparrows (*Passer domesticus*) have different size chest badges, with larger badges indicative of social dominance (photo credit: Christoph Moning; ML64183321). **(D)** Red-legged Partridges (*Alectoris rufa*) have throat patterns that serve as an indicator of individual quality (photo credit: Miguel Ángel Madrid Gómez; ML92730341). **(E)** Collared Flycatchers (*Ficedula albicollis*) have plumage patches involved in species recognition and in some populations are indicative of individual quality (photo credit: Christoph Moning; ML63455131). **(F)** Sunbitterns (*Eurypyga helias*) have eyespots on their wings that are used in territorial displays and to ward off interspecific competitors for food resources (photo credit: Dave Curtis; ML88770571). **(G)** Hooded Pitohuis (*Pitohui dichrous*) have aposematic plumage patterning and sequester toxins (photo credit: Frédéric Pelsy; ML206167861). **(H)** Paradise Tanagers (*Tangara chilensis*) and other thraupids have been the subject of comparative studies of the evolution of whole-body plumage patterns (photo credit: Zak Pohlen; ML32334281). **(I)** Fiery-necked Nightjars (*Caprimulgus pectoralis*) and other caprimulgids exhibit cryptic plumage patterns that aid camouflage (photo credit: Jacques Erard; ML204491951). **(J)** Marsh Seedeaters (*Sporophila palustris*) and other seedeaters have been the subject of genome-wide association studies that have identified genomic regions associated with plumage patterning (photo credit: Adrian Eisen Rupp; ML205344851).

intrinsically linked—such that patterning describes the location, shape, and size of different color patches on a feather or a bird's body—we do not review the function and quantification of avian coloration per se.

The importance of avian coloration (*sensu stricto*) in terms of its biological functions, evolutionary origins, and methods of quantification have been reviewed elsewhere at length (Burt 1981, Savalli 1995, Hill and McGraw 2006, Stoddard and Prum 2008, 2011; Burns et al. 2017, Cuthill et al. 2017, Witzel and Gegenfurtner 2018). In contrast, we feel that less attention has been spent on the biological function and origins of variation in the size, shape, and distribution of plumage patches, patterns, and patterning in birds and other animals (but see Pérez-Rodríguez et al. 2017). By highlighting recent conceptual and methodological advances, we hope our synthesis will inspire discussion and future studies regarding the biological role of plumage patterning in birds and provide general guidelines for how those patterns can be rigorously quantified and studied.

PLUMAGE PATTERNS AS INTRASPECIFIC SIGNALS

Variations in the size, shape, location, and regularity of plumage patches act as important signals among individual birds of the same species. Plumage patterns and patches convey information about an individual's age, sex, identity, location, social status, breeding condition, and other characteristics that mediate interactions among birds (Whitfield 1987, Lank 2002, Roulin 2004, Dale 2006). Much of our understanding about the role of plumage patterning comes from studies on a small number of tractable avian species, although the role that plumage patches play and the life history traits that they are associated with can vary widely. Associations among plumage patches and life history traits can even vary within species depending on the receiver, the signaler, and the signaling environment. In this section, we review formative studies regarding plumage patterns as intraspecific signals and discuss how recent studies have increased our understanding of how plumage patches facilitate communication within species.

Plumage Patterns as Signals of Sex, Age, and Identity

Many intraspecific signals convey information regarding the signaler's identity. Individual recognition lies at the core of social interactions and is particularly beneficial in species that have repeated interactions among individuals that gather in large aggregations (Tibbetts and Dale 2007). At a broader scale, plumage patches often designate the sex or age class of an individual (Humphrey and Parkes 1959, Booth 1990, Riegner 2008). Indeed, most species exhibit some degree of sexual dichromatism in coloration, patterning, or both (Eaton 2005, Burns and Shultz 2012), albeit to differing extents. Many ducks (Anatini) provide

examples of pronounced sexual dimorphism in plumage patterning (Scott and Clutton-Brock 1990, Omland 1997), such as the Mallard (*Anas platyrhynchos*), in which the male has bright, high-contrast plumage patches while the female has more uniform, mottled plumage. Other avian species, such as the Spotted Sandpiper (*Actitis macularia*), demonstrate more subtle, albeit diagnosable, sexual dimorphism in plumage patterning, in which females have fewer but larger spots on their chest than males (Blizard and Pruett-Jones 2017). Although sexually dimorphic plumage patterning is widespread in birds, differences in plumage patterning among age classes are perhaps even more common.

Essentially all bird species exhibit some level of difference in plumage patterning across age classes (Lawton and Lawton 1985, Pyle 1997, 2008; Howell 2010), although age-class differences in plumage patterning are especially pronounced in certain lineages, such as passerines (Rohwer et al. 1980, Moreno and Soler 2011), raptors (Pyle 2005a, 2005b; Clark and Pyle 2015; Figure 1A), and gulls (Dwight 1925, Grant 1986, Olsen 2018). Ontogenetic changes in plumage patterns are often associated with behavioral and ecological differences among life history stages that may help partition resources among individuals within a population (Booth 1990, Kokko 1997). For example, many gulls exhibit age-specific patterns of reproductive effort (Pugesek 1981, Reid 1988), while many passerines similarly acquire alternate breeding plumage well after fledging and only when adequate breeding conditions have been met. Thus, while the degree of age-related and sexual plumage pattern dimorphism varies among species, plumage patterns can serve to quickly identify an individual to a given sex or age class, which facilitates various social interactions.

While many species of birds likely identify individuals through vocal characters (Beer 1971, Krebs and Kroodsma 1980, Mammen and Nowicki 1981), certain species have plumage patterns that are extremely variable that serve to identify specific individuals within a larger group or population (Whitfield 1987). Perhaps the best example of this is the Ruff (*Calidris pugnax*), in which individual birds exhibit extreme variation in plumage patterning that is used during silent courtship and territorial interactions (Lank and Dale 2001, Hogan-Warburg 2002; Figure 1B). The ability to identify a specific individual via visual “fingerprints” (i.e. complex plumage patterns) generally becomes more beneficial in species with complex social interactions (Pollard and Blumstein 2011). In Ruffs, aggressive territorial encounters between “resident,” “marginal,” and “satellite” males are costly and decisions to engage in territorial disputes may be facilitated by rapid recognition of distinct plumage patterns (Lank and Dale 2001). More generally, accurate and rapid identification of specific individuals plays an important upstream role in many social behavioral pathways (Tibbetts and Dale

2007) and can be facilitated in part through variation in the size, shape, and spatial arrangement of plumage patterns. Beyond Ruffs, evidence for plumage pattern-based individual recognition has been demonstrated in Ruddy Turnstone (*Arenaria interpres*; Whitfield 1986) and Osprey (*Pandion haliaetus*; Bretagnolle et al. 1994), but remains somewhat limited in birds. Nonetheless, recent advances in image acquisition processing have advanced the field of “animal biometrics” (Kühl and Burghardt 2013, Duyck et al. 2015). These technological advances have enabled new avenues of research, such as the ability to remotely monitor individual penguins by the biometric “fingerprint” of unique black-and-white spots and bib patterns on the chest of each bird (Sherley et al. 2010). These advances have the potential to complement traditional banding, ringing, or other forms of individual physical tags to track individuals and their behavior.

Plumage Patterns as Signals of Social Dominance

While plumage patterns often communicate an individual's age, sex, or identity, variation in plumage patterns also facilitate agonistic intrasexual interactions among individuals in many species (reviewed in Senar 2006). Generally, more conspicuous or larger plumage patches are associated with more aggressive, socially dominant behavioral phenotypes (Santos et al. 2011). However, links between plumage patches, patterns, and life history traits are often context-dependent and may vary between phenological stages, age groups, or environmental conditions (Tibbetts 2008), which makes it difficult to generalize the role of plumage patches and their life history associations across species. Much of the pioneering work on the role of plumage patterns as signals of social dominance focused on a few, tractable avian systems, but ornithologists are increasingly studying different taxa to gain a deeper understanding of how plumage patterns mediate aggressive interactions.

One of the most well-studied systems involving plumage patches in ornithology is in the House Sparrow (*Passer domesticus*). Male House Sparrows have dark, high-contrast melanin chest patches, or “badges,” that vary in size (Møller 1988; Figure 1C). Badge size acts as a signal of social dominance that increases with age and physical condition (Møller 1987, Veiga 1993), such that larger badges are associated with increased dominance in male–male aggressive encounters and increased copulation rates (Møller 1990, Johnstone and Norris 1993, Liker and Barta 2001, Nakagawa et al. 2007). Similar associations are seen in other species, such as in the Great Tit (*Parus major*), in which the width of black breast stripes in males—sometimes called “ties”—is positively associated with increased social dominance (Järvi and Bakken 1984, Pöysä 1988) and territory defense (Norris 1990b, Quesada and Senar 2007). Additional examples are offered by bib size in the

Harris's Sparrow (*Zonotrichia querula*; Rohwer 1975), throat badge size in the Willow Tit (*Poecile montanus*; Hogstad and Kroglund 1993), bib size in the Sociable Weaver (*Philetairus socius*; Rat et al. 2015), among many others (Senar 2006, Santos et al. 2011). However, variation in the size of plumage patches is not always associated with social dominance. For example, the size of the white forehead patch of the well-studied Collared Flycatcher (*Ficedula albicollis*) is associated with success in territorial encounters in certain populations (Pärt and Qvarnström 1997), but not others (Garamszegi et al. 2006), indicating that associations between plumage patches and social dominance can differ widely—even among populations within the same species.

As indicated by the aforementioned examples, many studies linking plumage patches and patterns to intraspecific social dominance have identified a role for melanin-based rather than carotenoid-based patches (McGraw and Hill 2000, McGraw et al. 2002). However, associations between social dominance and carotenoid-based epaulet size in Red-winged Blackbird (*Agelaius phoeniceus*; Smith 1972, Røskaft and Rohwer 1987, but see Westneat 2006) and Red-shouldered Widowbird (*Euplectes axillaris*; Pryke and Andersson 2003) as well as positive correlation between the amount of yellow on the head and agonistic intrasexual interactions in Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*; Rohwer and Røskaft 1989) provide notable counterexamples. Thus, while there are more examples of the size of melanin patches mediating intrasexual conflicts in the literature, carotenoid-based patches can also play a role and sometimes bear stronger associations with aggression (Young et al. 2016).

Multiple plumage patches can sometimes act in concert to accentuate social dominance or to convey different social signals. For example, in addition to associations between the width of the black breast stripe and social aggression in the Great Tit (Järvi and Bakken 1984, Quesada and Senar 2007), the size or “immaculateness” of the white cheek patch among male *P. major* acts as an “amplifier” of the social dominance signal to further reinforce social dominance (Galván and Sanz 2008). Thus, in certain systems, multiple plumage patches may act in concert or synergistically to signal differences in social dominance or other life history traits in birds (Budden and Dickinson 2009, Chaine et al. 2011).

Plumage Patterns as Signals of Individual Condition or Quality

Beyond their role as signals of identity and social dominance, plumage patches and patterns are often targets of mate choice that mediate intersexual interactions (Hill 2006). Studies that have investigated the role of plumage patterns in mate choice as honest signals of individual

condition are variable in their approach: they include correlative field studies of unaltered wild birds (Marchetti 1998, Badyaev et al. 2001, Pryke et al. 2001, Masello and Quillfeldt 2003, Dunn et al. 2010), field studies of altered wild birds (Kose and Møller 1999, Pryke and Andersson 2003, Jouventin et al. 2008, Pardal et al. 2018), experimental studies of captive populations with unmanipulated plumages or manipulated plumage patterns and environmental conditions (Senar et al. 2005, Tarof et al. 2005, McGlothlin et al. 2007), or some combination of these strategies (Griggio et al. 2006). Collectively, these studies have demonstrated associations between the size and shape of various plumage patches and fitness metrics such as pairing success, copulation rates, extrapair paternity or cuckoldry rates, egg laying date, and immunity, among many others aspects of individual condition or mate quality (Hill 2006).

Associations between plumage patches and mate choice or individual quality are not universal, however. For example, Saether et al. (2000) found that variation in the amount of white on the outermost rectrices of Great Snipe (*Gallinago media*) is not associated with female choice, while Takahashi et al. (2008) found no association between the number of eyespots on the trains of male Indian Peafowl (*Pavo cristatus*) and mating success. Associations between plumage patches and fitness metrics can vary among populations, such as seen in the Common Yellowthroat (*Geothlypis trichas*), in which an association was found between mask size and mate choice in a Wisconsin population (Thusius 2001), while bib size was the inferred target of sexual selection in New York populations (Dunn et al. 2010). Furthermore, although the aforementioned studies on the House Sparrow were formative in recognizing the role of plumage patch sizes as signals of social dominance (Møller 1987, Veiga 1993, Nakagawa et al. 2007), subsequent studies have raised doubt about the “honesty” of badge-size signals involved in mate choice by failing to find a link between badge size and diet quality (Gonzalez et al. 1999), testosterone levels (Laucht et al. 2010), extrapair paternity rates (Cordero et al. 1999), or survivorship (Whitekiller et al. 2010). Studies on the Great Tit and variation in tie width and female reproductive success (Norris 1990a, 1993; Remeš 2011) provide another example of intensive study between plumage patterns as intraspecific signals in an avian system. Interestingly, a recent study demonstrated that increases in survival associated with wider breast stripes among Great Tits in forested habitats were actually reversed in urban environments (Senar et al. 2014), suggesting that links between plumage patches and life history traits are context dependent. Collectively, these studies reveal the difficulty in demonstrating the cost or investment associated with plumage patterns and idiosyncracies among systems (McGraw 2008, Weaver et al. 2017).

A large majority of the studies to date have focused on patch size as an indicator of social dominance or mate quality. There are other aspects of plumage patterns beyond size, and a smaller number of studies have found associations between aspects like plumage symmetry and patch regularity with indicators of individual condition, such as nutritional or developmental stress (Leung and Forbes 1996). For example, studies on the Zebra Finch (*Taeniopygia guttata*) have demonstrated female preference for male finches with symmetrical chest patterns (Swaddle and Cuthill 1994). Variation and possible preferences for symmetry in plumage patterns have also been studied in the Barn Swallow (*Hirundo rustica*; Møller 1992), European Starling (*Sturnus vulgaris*; Swaddle and Witter 1994), House Finch (Hill 1999, Badyaev et al. 2001), Rufous-tailed Scrub-Robin (*Cercotrichas galactotes*; Álvarez 2004), Little Bustard (*Tetrax tetrax*; Jiguet and Bretagnolle 2014), Common Waxbill (*Estrilda astrild*; Marques et al. 2016), and Northern Flicker (*Colaptes auratus*; Musgrove and Wiebe 2016), among others. Beyond symmetry and size, other plumage patterns have also been associated with indices of individual quality, such as the fractal geometry of bib plumage patterns in the Red-legged Partridge (*Alectoris rufa*; Bortolotti et al. 2006, Pérez-Rodríguez et al. 2013; Figure 1D). We explore advances in quantifying plumage patches in more detail later in the review.

PLUMAGE PATTERNS AS INTERSPECIFIC SIGNALS

Interactions among individuals of different species are common and drive the evolution of many adaptations. In addition to the role that plumage patterns play in transmitting information among individuals within a species, plumage patches also mediate interactions among species (Caro and Allen 2017). Many plumage patches comprise high-contrast patterns that call attention to an individual, whereas other plumage patches conceal birds. Plumage patches can also serve as deceptive signals that manipulate other species to the benefit of the signaler. In this section, we review the biological functions of plumage patches as interspecific signals. Although a greater number of studies have focused on plumage patterns as intraspecific signals, recent work has deepened our understanding of the various ways in which plumage patches and patterns mediate interspecific interactions among birds.

Patterning as Species Recognition

Many differences in coloration and patterning have been hypothesized to be under divergent sexual selection to avoid hybridization via character displacement (Mayr 1942, West-Eberhard 1983, Seddon et al. 2013, Hudson and Price 2014). This concept is sometimes referred to as the “Species Isolation Hypothesis” (McNaught and

Owens 2002), and is often invoked to explain interspecific differences in plumage patterns and the role of sexual selection in driving reproductive isolation among closely related species (Kraaijeveld et al. 2011, Janicke et al. 2018). Empirical evidence for the involvement of plumage patches and patterns in species recognition has come from diverse systems such as flycatchers in the genus *Ficedula* (Sætre et al. 1997; Figure 1E), the Chestnut-bellied Flycatcher complex (*Monarcha castaneiventris*; Uy et al. 2009a), and white-eyes in the genus *Zosterops* (Cowles and Uy 2019). Interspecific differences in plumage patterns have also been suggested as possible agents of reinforcement involved in the evolution of reproductive isolation in recent, rapid radiations such as southern capuchinos in the genus *Sporophila* (Campagna et al. 2017), redpolls in the genus *Acanthis* (Mason and Taylor 2015), and whistlers in the genus *Pachycephala* (Andersen et al. 2014), among others (Price 1998). Although the potential role of plumage patterning in species recognition and reinforcement is widely recognized in ornithology, empirical evidence has varied. Some studies have found elevated divergence in plumage patterns in sympatric species pairs compared to allopatric species pairs (Martin et al. 2015), whereas others have found no differences between sympatric and allopatric species pairs (McNaught and Owens 2002). At a macroevolutionary scale, Price-Waldman et al. (2020) found associations between rates of speciation and rates of plumage complexity evolution in tanagers, suggesting a role for plumage patterns in shaping broader patterns of speciation and diversification. Taken together, the role of plumage patterns in species recognition may differ widely among avian taxa and may interact with other targets of sexual selection, such as song, to act as a pre-mating barrier to gene flow via reinforcement when hybridization between species reduces fitness of the offspring.

Patterning as Mimicry

Occasionally, it is advantageous for organisms to bear a physical resemblance to another species in their ecosystem (Malcom 1990, Joron and Mallet 1998). Mimicry in birds often facilitates interspecific dominance (Prum 2014), and is acquired through the convergent evolution of broad-scale similarity in plumage patterning and coloration between the mimic and a sympatric, dominant species that acts as a model. A prominent example of interspecific mimicry is illustrated by similarity between the Hairy Woodpecker (*Dryobates villosus*) and the Downy Woodpecker (*Dryobates pubescens*), in which the smaller Downy Woodpecker gains an advantage over third-party competitors by resembling the larger Hairy Woodpecker (Weibel and Moore 2005, Prum and Samuelson 2012, Leighton et al. 2018). This phenomenon is not restricted to the genus *Dryobates*. Rather, a recent study revealed

that convergence in plumage patterns is widespread in woodpeckers and is likely related to interspecific mimicry and dominance in sympatry (Miller et al. 2019). Furthermore, interspecific dominance via mimicry has also been documented or suggested in diverse taxa such as cuckoos and hawks (Gluckman and Mundy 2013, Liang and Møller 2015), Old World orioles and friarbirds (Jönsson et al. 2016), toucans (Prum and Samuelson 2012), Neotropical flycatchers (Lopes et al. 2018), and many others (Prum 2014).

Plumage patches and patterns may also converge toward resembling more generalized visual signals involved in behavioral ecology. One example are “eyespot,” which are high-contrast, conspicuous plumage patches on the napes of many raptors that deter attackers, among other functions (Negro et al. 2007). One such example is provided by the Northern Pygmy-Owl (*Glaucidium californicum*), in which eyespots deter songbirds from mobbing the owl (Deppe et al. 2003). Similar conspicuous, high-contrast plumage patterns involved in agnostic interactions are seen on the wings of the Sun Bittern (*Eurypyga helias*) during its iconic frontal display (Frith 1978; Figure 1F).

Plumage Patterns as Aposematic Signals in Birds

Aposematic coloration, in which the signaler exhibits high-contrast patterning to warn predators against toxicity (Mappes et al. 2005), is extremely rare in birds. The only known example of avian aposematic coloration linked to toxicity occurs in members of the genus *Pitohui* (Dumbacher et al. 2008; Figure 1G), which have bright orange ventral and dorsal plumage that contrasts with black head, wings, and tail. Recent evidence suggests that similarities in plumage patterning and toxicity exhibited by the Hooded Pitohui (*Pitohui dichrous*) and the Southern Variable Pitohui (*Pitohui uropygialis*)—a rare example of Müllerian mimicry in birds (Dumbacher and Fleischer 2001)—may be the result of introgression from *P. dichrous* into the genomic background of *P. uropygialis* (Garg et al. 2019). Nonetheless, because sequestered toxins are themselves rare in birds, aposematic coloration is correspondingly rare as well, but may be limited more by the availability of food items that have the biochemical precursors of sequestered toxins than the ability of birds to sequester toxins (Jönsson et al. 2008).

Patterning as Camouflage

Predator–prey interactions influence the appearance of many animals (Thayer 1909, Cott 1940). An organism's survival is generally increased if it is difficult to locate by either predators or prey, and evolution has subsequently shaped the coloration and patterning of many species to avoid visual detection and recognition (Stevens and

Merilaita 2011). Rather than advertise a signaler's location, natural selection has shaped many plumage patterns to produce visual signals that are difficult to differentiate from an organism's background. Camouflage, or crypsis, encapsulates a suite of behavioral and physical traits that collectively minimize recognition and detection of an organism by a predator (Endler 1978). Background matching occurs when an organism expresses a color and pattern that is similar to a random sample of whatever substrate or background it is found on (Mottram 1916, Bortolotti et al. 2006). While color matching is arguably the most widely appreciated aspect of crypsis, patterning also contributes to camouflage. Prominent examples of the role of patterning in camouflage include disruptive coloration, or patterning that obscures the outline and shape of an organism (Cuthill et al. 2005); countershading, whereby animals are lighter ventrally than dorsally, which minimizes shadows and obscures 3-dimensional form (Tankus and Yeshurun 2009), and "dazzle" markings, which draw attention away from the outline of an organism to minimize recognition (Stevens et al. 2008). Even though these components of camouflage are widespread in birds and have evolved repeatedly in distantly related avian taxa, surprisingly little quantitative research has been performed on camouflage in birds compared to other vertebrates (Caro 2005, Harris et al. 2019). In mice, for example, extensive work has provided deep insights into various aspects of camouflage, including the fitness benefits of background matching in color (Vignieri et al. 2010), the evolutionary origin of adaptive color variants (Domingues et al. 2012), and the genetic architecture underlying variation in crypsis among murine rodents (Nachman et al. 2003, Hoekstra et al. 2006). Unfortunately, studies of comparable depth into the evolutionary origins and genetic underpinnings of camouflage in birds are lacking.

Much of the research done on plumage patterning and its role in camouflage in birds and other animals has historically relied on qualitative, human assessments of phenotypic and environmental variation (Stevens and Merilaita 2009). For example, Miller and Miller (1951) described geographic variation in the coloration and patterning of Western Screech-Owls (*Megascops kennicottii*) in qualitative and relative terms with respect to their potential role in camouflage: "paler, duller colored, less boldly striped Screech Owls should be less conspicuous on their daytime roosts in the desert vegetation... than birds in oak or oak-pine woods [with darker, bolder, and more varied markings]." Other studies of avian camouflage from the 20th century employed qualitative assessments of plumage patterning or conspicuousness in various avian systems and assumed links to environmental variation in soil or substrate color (Johnson 1972, Zink and Remsen 1986, Slagsvold et al. 1995, Dale and Slagsvold 1996).

Despite the widespread nature of avian camouflage, only recently have studies incorporated spectroscopy and calibrated measurements from digital photographs to more rigorously test quantitative associations between patterning and crypsis. In their study of 3 species of African nightjars, Troscianko et al. (2016b; Figure 1I) used digital photography to find that clutch survival was positively associated with background matching in terms of plumage patterning. Furthermore, escape distance increased when the plumage patterns of adult nightjars was poorly matched to their visual background (Wilson-Aggarwal et al. 2016), suggesting that some birds may be able to assess their own level of background matching and choose optimal roosting sites accordingly (Stevens et al. 2017). In addition to this recent series of studies on African nightjars, there have been a plethora of studies focused on egg patterning and coloration and their role in camouflage, mimicry, and clutch survival (Stoddard et al. 2014, 2016; Troscianko et al. 2016a, Gómez et al. 2018). Aside from the aforementioned studies, there have been remarkably few rigorous quantifications of background matching among populations or species of birds with respect to plumage patterning.

In addition to reducing the chance of visual detection by predators through camouflage, plumage patterning can reduce the chance of predation by disorienting or deceiving the signaler's escape velocity (Stevens et al. 2008, Scott-Samuel et al. 2011, von Helversen et al. 2013). In particular, high-contrast patterns, such as adjacent black and white patches, bars, or stripes, can produce visual illusions that interfere with visual assessments of motion and reduce the chance of successful capture (Brodie 1992). For example, field observations and experiments have demonstrated that white rump patches on Rock Pigeons (*Columba livia*) reduce the chance of capture by Peregrine Falcons (*Falco peregrinus*) compared to plumages that lack a white rump patch (Palleroni et al. 2005).

EVOLUTIONARY HISTORY OF PLUMAGE PATTERNS

The phenotypic diversity and biological functions of plumage patterns are the products of over 100 million years of archosaur evolution (Li et al. 2010, Vinther 2015). As highly modified integumentary appendages, feathers are keratinous structures with diverse developmental pathways that have been the subject of over 150 yr of intensive study (Dyck 1985, Prum and Brush 2002). More recently, advances in phylogenetic comparative methods, evolutionary developmental studies, and genome-wide association analyses have enabled new lines of research regarding the evolutionary history and elucidation of the genetic architecture underlying plumage patterns. In this section, we review progress from macroevolutionary

studies that span many species and deep evolutionary time scales to studies that are focused on more recent evolutionary events among closely related species, populations, or individuals that differ in plumage patterns.

Phylogenetic Comparative Studies of Plumage Patterns

Comparing plumage patterns among related species in a phylogenetic framework has shed light on the evolutionary history underlying gains, losses, and changes of plumage patterns and patches. Phylogenetic comparative studies of plumage patterning have been undertaken at different scales: some have focused on a relatively small number of related species or genera (e.g., Price and Pavelka 1996, Omland and Lanyon 2000, Maia et al. 2016, Ligon et al. 2018, Soma and Garamszegi 2018, Eliason et al. 2019, Cicero et al. 2020, Merwin et al. 2020), while others have examined large, macroevolutionary patterns of plumage evolution across hundreds or thousands of species (e.g., Riegner 2008, Gluckman and Cardoso 2010, Mason et al. 2014, Dale et al. 2015, Somveille et al. 2016, Galván et al. 2017, Shultz and Burns 2017, Cooney et al. 2019, Marcondes and Brumfield 2019, Price-Waldman et al. 2020). Collectively, these studies have revealed an array of evolutionary patterns as diverse as the focal taxa themselves, but do suggest a role for plumage patterning in shaping patterns of avian diversification (Price 1998, Price-Waldman et al. 2020).

The ability to develop and produce plumage patterns within individual feathers—such as scales, bars, mottling, and spots—is more prevalent in certain clades (e.g., Phasianidae, Accipitridae, Estrildidae). Specific patterns sometimes only appear on certain body parts (i.e. dorsal or ventral regions) and pattern types (i.e. streaks, bars, countershading) exhibit broad associations with body size among birds (Riegner 2008). Furthermore, intrafeather (i.e. within-feather) patterns have evolved repeatedly in different taxonomic groups of birds from an ancestral state that did not express scales, bars, or spots (Gluckman and Mundy 2016). Lineages with pronounced ecological differences (e.g., Anseriformes and Galliformes) can exhibit similar rates of evolutionary transition between intrafeather plumage pattern states, suggesting developmental constraints may be similar across clades (Gluckman and Mundy 2016), but can still vary in association with behavioral or ecological differences among groups (Marshall and Gluckman 2015). While barred plumage has been proposed to promote camouflage (Endler 1978, Gluckman and Cardoso 2010), broad-scale variation in intrafeather patterns is not associated with open or closed habitat categorizations (Somveille et al. 2016). These macroevolutionary studies speak to broad, generalized patterns across deep evolutionary time scales, but associations between plumage patterns within individual feathers and other life

history characters are more nuanced when specific avian lineages are examined in isolation.

Phylogenetic comparative studies have also illuminated how patterning has evolved in birds through changes to entire plumage patches or feather tracts in addition to plumage patterns within a single feather. Different studies have uncovered varying associations between plumage patterns among patches and lighting conditions (Marchetti 1993, Gomez and Théry 2004, Shultz and Burns 2013), whereas the ability of an organism to produce certain coloration mechanisms based on molecular structures also influences plumage patterns and color diversity across a bird's body (Maia et al. 2013, Mason et al. 2014, Eliason et al. 2019). Changes in patterns that involve structural colors, which involve rearrangements in the keratin–melanin matrix that comprises feathers (Jawor and Breitwisch 2003), are generally less constrained by developmental pathways compared to carotenoid-based patterns, which may require biochemical changes to carotenoid sequestration and modification pathways (Morrison and Badyaev 2016).

Many phylogenetic comparative studies have focused on sexual dichromatism, with a special emphasis on how plumage patterns differ between sexes and how those differences have evolved at different taxonomic scales (Burns 1998, Hofmann et al. 2008, Maia et al. 2016, Kearns et al. 2020). For example, Shultz and Burns (2017) demonstrated that evolutionary changes in both male and female plumage patterns contribute to variation in sexual dichromatism among more than 300 species of tanagers, implicating both natural and sexual selection as drivers of sexual dimorphism in plumage patterns.

Other macroecological studies have similarly shown that plumage patterns are subject to a wide array of selective pressures, including both natural (e.g., camouflage) and sexual (e.g., badges) selection, and that selection pressures can act on different plumage patches independently (Dale et al. 2015, Dunn et al. 2015, Maia et al. 2016, Cooney et al. 2019, Merwin et al. 2020, Price-Waldman et al. 2020). Additional phylogenetic comparative studies of plumage patches and patterns are needed if stronger generalizations are to be drawn across birds and if we are to understand the evolutionary and ecological contexts that characterize exceptions to these generalizations.

Genome-wide Association Studies of Plumage Patterning

Alongside rapid advances in DNA sequencing technology and bioinformatics, the past decade has borne witness to major advances in our understanding of the genetic architecture of plumage coloration and patterning (Toews et al. 2016a, Funk and Taylor 2019). Genome-wide association studies among phenotypic morphs or closely related taxa have identified

various genes involved in both broad-scale patterning of differences among plumage patches or feather tracts and localized patterns within feathers (Ekblom and Galindo 2011). Certain biomolecular pathways underlying avian coloration, such as the melanogenesis pathways that generate eumelanin and pheomelanin, are largely conserved among vertebrates (Hubbard et al. 2010, Galván and Solano 2016). However, changes in the expression patterns or amino acids within protein-coding exons of over 30 related genes in the melanogenesis pathway can produce convergent phenotypes that appear very similar at the organismal level (Manceau et al. 2010, Harris et al. 2019).

Prior to high-throughput sequencing, studies relied heavily on a candidate-gene approach to uncover associations between patterns of melanism at the organismal level and mutations within well-characterized genes. In particular, the large majority of early candidate gene studies focused on associations between melanocortin-1 receptor (MC1R) and melanin-based plumage variants (Mundy 2005). Collectively, these studies have either found associations (Theron et al. 2001, Mundy et al. 2004, Uy et al. 2009b, Gangoso et al. 2011, Baião and Parker 2012, Cibois et al. 2012, San-Jose et al. 2017) or have not found such associations (MacDougall-Shackleton 2003, Cheviron et al. 2006, Bourgeois et al. 2012, Dobson et al. 2012) between a small number of candidate genes and variation in melanin-based phenotypes. Powered by high-throughput sequencing, an increasing number of recent studies have identified associations between melanin-based plumage patterning and genetic differences in or near an expanding assortment of genic regions, such as melanocortin-1 receptor (MC1R), agouti signaling protein (ASIP), tyrosinase (TYR), tyrosinase-related protein 1 (TYRP1), and KIT ligand (KITLG), among other candidate loci (Delmore et al. 2016, Toews et al. 2016b, Campagna et al. 2017, Stryjewski and Sorenson 2017, Abolins-Abols et al. 2018, Funk and Taylor 2019). Interestingly, many of the aforementioned genomic studies have identified associated loci outside of protein-coding regions of the genome, implying that variable sites in promoter or cis-regulatory elements often underlie changes in plumage patterning that involve individual patches, such as black throat color in wood warblers (Toews et al. 2016b, Baiz et al. 2020) and mosaic melanin patterning of different plumage patches in southern capuchinos (Campagna et al. 2017) and munias (Stryjewski and Sorenson 2017). While melanogenesis is one of the better-characterized biochemical and genetic pathways in vertebrate evolutionary developmental biology, many discoveries regarding the genetic architecture of avian plumage patterns based on other pigments, such as carotenoids, have also been made in recent years.

Carotenoids are pigments derived from birds' diets and undergo a wide array of biochemical changes between the time they are ingested and when they are deposited in growing feather follicles (Badyaev et al. 2015, Ligon et al. 2016, Morrison and Badyaev 2016). Changes in the biochemical and developmental pathways underlying carotenoid processing and deposition contribute to the wide array of carotenoid molecules observed in birds (e.g., lutein, rhodoxanthin, β -carotene) that collectively produce the bright red, yellow, and orange plumage patches and patterns seen across birds (Toews et al. 2017). Recent studies have identified genes associated with enzymes that alter the biochemical composition of carotenoids and the resulting pigments deposited in feathers, providing a mechanistic framework for variation between red and yellow plumage in birds (Lopes et al. 2016). In particular, a group of genes associated with the enzyme cytochrome P450 has been implicated in carotenoid modifications in various systems such as finches (Mundy et al. 2016, Toomey et al. 2018, Kim et al. 2019), warblers (Toews et al. 2016b, Brelsford et al. 2017), and canaries (Lopes et al. 2016), and likely plays a role in other carotenoid-based polymorphisms (e.g., McGraw et al. 2003). Given the large number of biochemical changes and different carotenoid types that underlie variation in carotenoid-based plumage patterning, one might expect a larger number of genes and associated regulatory elements to be associated with variation in carotenoid-based patterning compared to melanin pigments, which are restricted to pheomelanin and eumelanin. While the large majority of bird pigmentation is based on melanin and carotenoid deposition in feathers, the genetic architecture of variation in other pigment types has also been advanced, such as identification of loci controlling psittacofulvin deposition in parrots (Cooke et al. 2017). That said, there is still much to be learned regarding the genetic architecture and biochemical pathways underlying other rare avian pigments, such as porphyrins, pterins, flavins, and other undescribed pigments (McGraw 2006). While the aforementioned gene-association studies have provided strong evidence for a role of various genes in melanin and carotenoid deposition, it is often difficult to demonstrate causality or a functional link between the gene and phenotype at hand. Fortunately, evolutionary developmental studies are also advancing our functional and mechanistic understanding of how plumage patterns within and among feathers develop and evolve.

While protein coding genes and changes in patterns of gene expression are widely appreciated as drivers of phenotypic evolution, structural variants (sometimes called "supergenes" when large chromosomal inversions are involved) are gaining increasing attention as important contributors to phenotypic diversity (Wellenreuther and Bernatchez 2018). In birds, a growing number of studies

have identified chromosomal inversions that are associated with changes in plumage patterning (Taylor and Campagna 2016), such as differences between tan and white morphs of White-throated Sparrow (*Zonotrichia albicollis*; Huynh et al. 2011, Tuttle et al. 2016), large-scale variation in plumage patterning (and associated reproductive strategies) in Ruffs (Küpper et al. 2016, Lamichhane et al. 2016), and patterning differences between Hooded Crows (*Corvus cornix*) and Carrion Crows (*Corvus corone*; Poelstra et al. 2014). Depending on the size of the chromosomal inversion and the extent of linkage disequilibrium involved, inversions and other structural chromosomal variants have the capacity to induce large-scale changes to plumage patterns and other linked phenotypes (Wellenreuther and Bernatchez 2018). Copy-number variants can also play a role in plumage pattern variation as was recently demonstrated in the Rock Pigeon. Certain pigeon breeds have irregular, speckled plumage patterns with increased white that are associated with increased copy number of the Z-linked *St* locus compared to wildtype pigeons. Additional copies of the *St* locus alter the expression of various genes involved in the melanogenesis pathway and reduce the deposition of eumelanin in pigeon feathers (Bruders et al. 2020). Although birds are thought to generally exhibit strong synteny and conservation of chromosomal structure at a broad scale, as genomic resources of non-model taxa continue to improve, we will surely find additional examples of structural variants—such as chromosomal rearrangements and copy-number variants—driving variation in avian plumage patterns.

Evolutionary Developmental Biology of Plumage Patterns

The generation of plumage patterns is intricately tied to the evolutionary developmental biology of feathers (Prum and Brush 2002). In addition to genome-wide association studies, advances in our understanding of the evolutionary history of plumage patterns have been spurred by advances in molecular techniques outside of DNA sequencing and functional approaches (Haupaix and Manceau 2019). In this section, we summarize some of the major recent advances that have used experimental and developmental approaches to understand the genetic architecture of plumage patterns. Variation in plumage patterns among body parts, such as the rump or belly of a bird, are first organized by the designation of feather tracts (Chen et al. 2015). Meanwhile, patterns within feathers, such as spots and bars, are generated via the fine-scale spatial and temporal deposition of melanin during feather growth (Galván et al. 2017). Reaction–diffusion models (also known as “Turing” models) comprise a mathematical and theoretical framework that has played a central role in our understanding of the spatiotemporal development of animal

integumentary patterns (Turing 1952, Kondo 2002, Kondo and Miura 2010), including within-feather patterning (Price and Pavelka 1996, Prum and Williamson 2002) and patterning among feather patches and tracts (Neguer and Manceau 2017). In brief, reaction–diffusion models approximate the concentration of certain molecules (i.e. reactions), and how those molecules spread over space and time (i.e. diffusion). As feather follicles grow and develop in a tubular sheath, complex biochemical pathways and molecular interactions generate positional cues that dictate when and where melanosomes should be incorporated into keratinosomes along barb ridges via phagocytosis (Watterson 1942, Yu et al. 2004, Mills and Patterson 2009). Reaction–diffusion dynamics have been used to explain a growing number of different aspects of plumage patterning, including spacing between feather follicles within a feather tract (Jiang et al. 2004), as well as oscillations between states of activation and inhibition of particular cell types and states that generate periodic episodes of melanin deposition (Prum and Williamson 2002, Neguer and Manceau 2017). A recent comparative study across 10 species of galliforms revealed interspecific variation in yellow and brown stripe width in juveniles that follows expression of ASIP in the somatic mesoderm of chicks, in accordance with reaction–diffusion models of spatial arrangement and temporal deposition of melanin (Haupaix et al. 2018).

While major advances in our understanding of the evolutionary development and genetic architecture of plumage patterning have been made, functional validation of genetic variants is still very challenging in birds compared to other taxa. First, captive populations of wild birds are difficult to establish and maintain. Changes in gene expression, which appear to underlie many of the aforementioned genotype–phenotype associations, are specific to certain tissues and developmental stages, such that ontogenetic series are required to pinpoint when, where, and at what age differential gene expression occurs. Model avian systems such as chicken (*Gallus gallus*), Zebra Finch, Japanese Quail (*Coturnix japonica*), and other captive birds provide tractable systems for ontogenetic studies of gene expression and function, but are distantly related from many species of interest. Furthermore, gene editing technologies that have become popular validation tools in evolutionary developmental studies have seen limited use in birds because of the difficulty of accessing single-cell embryos or primordial germ cells (Woodcock et al. 2017). Nonetheless, our ability to create knock-out or knock-in genetic variants in birds is constantly improving, thanks to continued innovations in genome-editing tools such as transcription activator–like effector nuclease (TALEN; Cermak et al. 2011, Park et al. 2014) and clustered regularly interspersed short palindromic repeats (CRISPR; Doudna and Charpentier 2014, Véron et al. 2015, Oishi et al. 2016),

and our ability to isolate, manipulate, and propagate primordial germ cells from birds (Cooper et al. 2018). While genome-editing studies are currently restricted to chicken, Zebra Finch, and Japanese Quail, innovative techniques will hopefully expand genome-editing tools to non-model organisms. Looking ahead, combining evolutionary developmental biology with high-throughput DNA sequencing and bioinformatics will surely uncover exciting new discoveries regarding the genetic architecture of plumage patterning.

OF PLUMES AND PIXELS: QUANTIFYING PLUMAGE PATTERNS VIA DIGITAL PHOTOGRAPHY

Studies of avian coloration and patterning have benefited immensely from recent technological advances in color science and computer vision. For centuries, assessments of avian coloration and complex plumage patterns were largely subjective (Endler 1990). Ridgway's (1912) seminal work on ranking and matching colors to widely used color standards represented a large step forward toward objective quantifications of color, but descriptions of color—and plumage patterns—were largely based on expert opinions of taxonomists and subjective comparisons until relatively recently (Rosenthal 2007). Single plumage patches that are large and conspicuous, such as the large, black breast stripe present on Great Tits, have been measured using simple estimations of area via different combinations of manual measurements for decades (Figueroa and Senar 2000). More recently, digital photography has been incorporated into studies of plumage patches with increasing frequency and sophistication (Stevens et al. 2007, McKay 2013). In this section, we explore recent developments in the integration of photography and plumage patterning by focusing on new methods, software packages, and computer code. We compare and contrast various modern approaches to quantifying plumage patterns, compare their output, and consider their strengths and weaknesses (Table 1). We do not discuss spectrophotometric methods because they are largely confined to point estimates of reflectance rather than spatial analyses of color variation that are essential to analyses of plumage patterns (but see Burns et al. 2017 for review of spectrophotometry). However, we do recognize that spectral analyses involving spectrophotometry do allow for more fine-scale estimation of reflectance across different wavelengths of light, whereas estimates of reflectance spectra acquired via digital photography are interpolated from a much smaller number of reflectance estimates across wavelengths. Thus, if a research question involves discriminating between spectral curves of plumage patches, some combination of spectrophotometry and photography is likely a better solution than photography alone. ImageJ (Abràmoff et al. 2004, Schneider

et al. 2012) and R (R Core Team 2020) are two open-source environments that have revolutionized image science and are both widely used across biology. Both computational environments enable different components of repeatable, accurate, automated pipelines to measure plumage patterns represented by digital images.

Recently, an assortment of ImageJ and R plugins have been developed specifically for analyzing animal coloration and patterning that have greatly advanced the ease by which users can obtain sophisticated, repeatable measurements of plumage patterns (Troschianko and Stevens 2015, Van Belleghem et al. 2018, Chan et al. 2019, Maia et al. 2019, Berg et al. 2020). These products represent “higher-level” computer programs and functions that are developed with code from other packages and developers; thus, while they enable measurements to be quickly and accurately acquired for empiricists, they also provide the framework for further methods development and refinement for users with the capacity to dissect and modify code. The aforementioned programs differ in what aspect of image capture, processing, and analysis they can perform, but there is also substantial overlap in what they can accomplish (Table 1). These methods are quite new and their usage in birds has been limited thus far, but the ease and sophistication of these image filters and image segmentation algorithms will undoubtedly reveal new insights into the evolution and ecology of avian plumage patterns.

Here, we describe some readily available options for 2 main phases of plumage pattern analysis: (1) plumage pattern segmentation and (2) plumage pattern quantification. Each workflow will vary in some way based on existing infrastructure and available resources, but new user-friendly pipelines are enabling more and more researchers to accurately quantify plumage patterns both in the field and in controlled settings. Programs such as the Multispectral Image Calibration and Analysis Toolbox (MICA; Troschianko and Stevens 2015) provide extensive functionality to pre-process and prepare “multispectral images” for downstream processing and analysis, and we direct readers to other studies for more information on camera and photography set-up considerations (McKay 2013, Troschianko and Stevens 2015, Berg et al. 2020).

Recently, Berg et al. (2020) published an analytical pipeline entitled Quantitative Colour Pattern Analysis (QCPA) that provides an open-source, user-friendly framework to perform each step of a modern plumage pattern quantification workflow, including image acquisition and processing, to image segmentation, and pattern analysis. As a set of algorithms available as an ImageJ plug-in, QCPA builds on MICA (Troschianko and Stevens 2015) and PAT-GEOM (Chan et al. 2019) to provide a promising framework for plumage pattern quantification. Here, we discuss various options in image segmentation and pattern

TABLE 1. Summary of image segmentation and pattern analysis methods, including brief description, strengths, considerations, and programs that provide each method.

Method goal	Method name	Description	Strengths	Considerations	Program
Segmentation	Thresholding	Pixels are binned into 2 or more categories based on whether they are above or below a threshold value (brightness for a grayscale image or RGB values for color images) to create a binary or discrete image.	Computationally fast; can handle uniform images (i.e. all black plumage patch) compared to <i>k</i> -means clustering.	Requires arbitrary designation of threshold(s) to delimit pixel bins. Does not incorporate information about adjacent pixels or transitions among pixels.	<i>patternize</i> (Van Belleghem et al. 2018) ImageJ (Schneider et al. 2012)
Segmentation	<i>k</i> -means clustering	RGB values (or other channels post processing) are used to iteratively assign pixels to one of <i>k</i> different groups that minimizes the difference between each pixel and the cluster centers (Hartigan and Wong 1979). Pixels of binary/grayscale images are assigned to "basins" of brightness values and the "ridges" separating those basins are estimated. Filters such as Gaussian blurs are often applied ahead of time to smooth edges and facilitate ridge identification.	Highly adaptable method of image segmentation that can accommodate more than two colors.	Number of clusters is usually defined manually (but can be optimized), may not work well with colors that differ only slightly or blend together in a gradient.	<i>patternize</i> (Van Belleghem et al. 2018) Pavo (Mala et al. 2019)
Segmentation	Watershed segmentation	Sequentially group or separate adjacent pixels according to experimentally determined thresholds of spatial and chromatic acuity. Series of functions that allow users to determine size, number, shape, orientation, and distribution of markings. Estimate the number of transitions between color classes along body axes based on transition matrices.	Useful for high-contrast, two-color patterns. Incorporates information from adjacent pixels to form a "gradient map."	Requires some manually determined parameters to delimit patterns accurately on case-by-case basis.	<i>patternize</i> (Van Belleghem et al. 2018)
Segmentation	Receptor Noise Limited Filtering and Clustering		Incorporates avian visual models of spectral and spatial sensitivity.	Thresholds must be manually set but can be adjusted based on information from behavioral studies.	Quantitative Colour Pattern Analysis (Berg et al. 2020)
Pattern analysis	Pattern geometry analysis		Versatile analyses applicable to a wide array of patterns.	Images should be standardized for lighting conditions, area, orientation, and resolution. Best suited for high-contrast markings.	Pat-geom (Chan et al. 2019)
Pattern analysis	Color adjacency analysis		Useful, simple method for quantifying repeating patterns along a body axis, such as bars or streaks.	Relatively little use to date in visual ecology, requires manual fine tuning of some parameter choices. Only considers the frequency of color shifts, not intensity of contrast. Less useful for patterns that do not follow body axes.	Quantitative Colour Pattern Analysis (Berg et al. 2020)

Table 1. Continued

Method goal	Method name	Description	Strengths	Considerations	Program
Pattern analysis	Visual contrast analysis	Leverage transition matrices of chromatic and achromatic values to estimate overall conspicuousness.	Size, position, hue, saturation, and brightness of plumage patches and patterns all considered simultaneously under an avian visual model.	Examines plumage patches as a composite whole, does not consider elements separately.	Quantitative Colour Pattern Analysis (Berg et al. 2020)
Pattern analysis	Boundary strength analysis	Estimates the intensity of patch edges for either chromatic or luminosity pixel values. The mean and standard deviation of these receptor noise estimates correspond to visual stimulation and salience.	Metrics are rooted in sensory ecology of visual signals, can be used on both foreground subjects and visual backgrounds. Can separate chromatic and achromatic elements or consider together.	Relies on a segmented image with clearly delineated (clustered) color pattern elements. Output does not include information about size, shape of pattern. Output pertains solely to color and luminosity boundaries and the contrast therein.	Quantitative Colour Pattern Analysis (Berg et al. 2020)
Pattern analysis	Fast Fourier Transform	Widely used algorithm in processing various kinds of signals (e.g., visual, sound). For images, it performs a granularity analysis that calculates spatial frequency differences at different pixel values or levels. Images with higher energy across levels have more “features” or pixels that have high value differences compared to other nearby pixels.	Can produce a single metric that describes variation in the number and spatial arrangement of features (i.e. bars, spots).	Pattern complexity is reduced to a single metric, does not provide more detailed information on the size, shape, or where features occur. Users must indicate which values (pixel sizes) will be included in estimating energy.	Multispectral Image Calibration and Analysis Toolkit (Trosianko and Stevens 2015)
Pattern analysis	Scale-invariant feature transform (SIFT)	Performs a series of image filters that isolates features from within an image and assigns a vector to each feature that has magnitude and directionality.	Provides consistent output regardless of orientation, scaling, rotation, or lightness of an image. Based on models of cerebral cortex function in mammalian vision.	Does not provide information on size, shape, or regularity in pattern. Used mostly in pairwise comparisons to identify closest matches.	NaturePatternMatch (Stoddard et al. 2014)

analysis with special attention toward plumage patterns in birds following best practices recommended by software developers and visual ecologists (Berg et al. 2020).

Plumage Pattern Segmentation

Following image acquisition, linearization, alignment, and other “pre-processing” steps (see Troschianko and Stevens 2015 for detail), the next step in pattern analysis is typically image segmentation. Image segmentation divides an image into a simplified set of “regions” or groups of pixels for downstream analysis. At the most basic level, users can delimit plumage patches by generating polygons by hand, as was recently done to quantify variation in the streaking of undertail coverts among redpoll finches (*Acanthis* spp.; Mason and Taylor 2015). We do not recommend this method because it is subjective, is based on human vision rather than an avian visual system, and becomes quickly intractable with large data sets. Fortunately, a wide variety of automated or semi-automated methods exist to help expedite segmentation of images taken from specimens or live birds. Here, we briefly describe some of these methods and their implementation in quantifying plumage patterns.

Thresholding is perhaps the simplest method of image segmentation (Arifin and Asano 2006). In thresholding, pixels are assigned to one category or another based on whether they are above or below a certain value. Many threshold filters are based on a single value, such as brightness or stimulation of a specific channel or cone type (i.e. double cone receptor). More complex thresholding formulas may involve multiple channels or cones, and can bin pixels into two channels or more as determined by the user. As such, thresholding is flexible, but may require substantial human input to be accurate, especially when plumage patterns are variable among individuals, such as studies that involve comparisons among populations or species. Nonetheless, thresholding can still be effectively and efficiently applied to image segmentation in many systems—especially high-contrast patterns such as the area of white head spots in the Superb Bird-of-Paradise (*Lophorina superba*; McKay 2013)—and can be accessed via tools such as *patternize* (Van Belleghem et al. 2018) and ImageJ (Schneider et al. 2012).

K-means clustering is widely used in statistical analyses and offers another option for image segmentation, in which pixels are binned into one of K clusters that minimizes the color distance between the pixel and a cluster's center (Steinley 2006). The number of clusters (K) is typically set by the user, but this number may require fine-tuning for low-contrast colors that are similar and may blend together. Users may use a reference image, as implemented in *patternize* (Van Belleghem et al. 2018) and *pavo* (Maia et al. 2019), or may cluster pixels without a reference, but then users must ensure that homologous patches are compared in downstream analyses. K -means

clustering is widely adaptable to many pipelines, but can generate artifacts when the number of clusters (K) is higher than the actual number of colors involved (i.e. if $K = 2$ is used on a uniform plumage patch). Recently, Berg et al. (2020) developed a method that leverages naïve Bayesian clustering (Domingos and Pazzani 1997) to allow users to interactively delineate clusters as an alternative segmentation method incorporated into their QCPA workflow.

The watershed transformation is another widely applied algorithm for image segmentation, especial in medical and material sciences (Beucher 1991, Kornilov and Safonov 2018). The term “watershed” is a topographical analogy, by which water (i.e. brightness) travels along “ridges” (i.e. bright regions) and is collected in “basins” (i.e. dark regions), such as the spots on the ventral side of Spotted Sandpipers (Blizard and Pruett-Jones 2017). Many watershed segmentation workflows incorporate filters such as Gaussian blurs to reduce noise and more clearly delineate regions of interest. Furthermore, watershed algorithms require binary (i.e. grayscale) images and are therefore best suited for high-contrast, repeated patterns against a uniform background, such as dark spots among otherwise white feathers. Overall, watershed segmentation is an effective way to detect simple plumage patterns that takes into account information in adjacent pixels, but may also require manual fine tuning of filters and image transformations to optimize workflows and accurately segment plumage pattern images. Watershed segmentation is available through tools such as *patternize* (Van Belleghem et al. 2018) and ImageJ (Schneider et al. 2012).

Recently, (Berg et al. 2020) developed a novel method of image segmentation that incorporates an avian visual model of spatial acuity and color differentiation known as “Receptor Noise Limited Clustering” (RNLC). First, an optional filter (e.g., Gaussian blur) can be applied to approximate the visual model of the intended receiver and restore sharp edges between color boundaries. Then, an agglomerative hierarchical clustering approach is used to group pixels, in which differences in color and luminosity between adjacent pixel clusters are iteratively calculated and compared to “just-noticeable” threshold differences that are based on behavioral experiments of visual receptors (Vorobyev and Osorio 1998, Vorobyev et al. 2001). The RNLC method is available via the QCPA plug-in (Berg et al. 2020) in ImageJ and offers a promising segmentation method that incorporates an avian visual model into an open-source, user-friendly data processing pipeline.

Plumage Pattern Quantification

Once images have been segmented and the features of interest (i.e. spots, bars) have been isolated from their background, users have various options to quantify variation in plumage patterns. There is no single option that is best suited for all studies; rather, users should consider their

end goal and identify which method provides the output that best matches the question at hand. Here we summarize a few of these options, describe their various outputs, and identify systems for when they may be best suited (summarized in Table 1).

Perhaps the most simple and intuitive option to quantify plumage patterns is to calculate metrics related to the number, size, shape, orientation, and distribution of plumage patches. Following segmentation, users can easily calculate a number of basic geometric features using the PAT-GEOM plugin for ImageJ (Chan et al. 2019), which calculates seven geometric properties of plumage patterns. These properties can then be used to compare “average patterns” among individuals, populations, or species. These metrics are best suited for discrete, high-contrast patterns, and photographs should be taken under best practices to ensure that measurements are comparable across photographs.

Beyond basic estimates of pattern geometry, there are various more complex estimates of plumage patterns. Many plumage pattern methods generate what are known as “transition matrices” to estimate the number, character, and strength of transitions between different color classes or patterns, including color adjacency analysis (Endler 2012), visual contrast analysis (Endler 1991, Endler and Mielke 2005), and boundary strength analysis (Endler et al. 2018). In brief, color adjacency analysis estimates the number of transitions along both the perpendicular and parallel axes of an organism’s body (Endler 2012) and has not seen extensive use in visual ecology but has been applied in landscape ecology (McGarigal and Marks 1995). As a more holistic measure of patterning, visual contrast analysis combines spatial, chromatic, and achromatic properties of plumage patterns to estimate overall “conspicuousness” of color patterns (Endler 1991). Properties such as the size, position, hue, saturation, and brightness of plumage patches and patterns are all considered simultaneously under an avian visual model to collectively describe the conspicuousness of entire plumage patterns “as birds see them” (Endler and Mielke 2005). Finally, boundary strength analysis offers another estimate of plumage pattern based on receptor noise thresholds to estimate the contrast between adjacent plumage patches, which can be summed across an entire region of interest to estimate total conspicuousness, as demonstrated in Gouldian Finches (*Erythrura gouldiae*; Endler et al. 2018). While these methods offer an objective way to quantify plumage pattern under the appropriate visual model, they have seen limited use in part because of difficulties in implementing the formulas involved. All three of these methods are now included in the QCPA pipeline and can be incorporated into plumage pattern studies with relative ease (Berg et al. 2020).

Fast Fourier Transforms (FFT) are widely used in signal processing as a way to quantify periodicity in complex composite signals of various kinds, including animal patterns (Godfrey et al. 1987, Stoddard and Stevens 2010, Troscianko et al. 2016b). In brief, FFTs are based on our understanding of neurophysiological processing of spatial patterns in vertebrates and involve a series of filters applied at increasing spatial frequencies to quantify oscillations in pixel values. FFT filters are typically applied to single channels or cone-catch values related to pattern detection, such as double-cone receptors in birds, which are sensitive to changes in brightness or reflectance (Hart 2001, Osorio and Vorobyev 2005). The amplitude of change at different spatial scales is referred to as “energy” or “power” and describes variation from uniformity to conspicuousness. FFT filters have recently been used to describe variation in the plumage patterns of roosting nightjars, coursers, and plovers (Wilson-Aggarwal et al. 2016, Stevens et al. 2017). The output of FFTs provides informative metrics that describe overall patterning, which can then be compared among individuals or against visual backgrounds to elucidate the role of plumage patterns in avian visual ecology.

Additional, “higher-level” methods exist that incorporate various image transformations or algorithms to quantify variation in plumage patterns. One such option is offered by NaturePatternMatch (Stoddard et al. 2014), which leverages the Scale Invariant Feature Transform (SIFT; Lowe 1999) to characterize animal patterns in a framework inspired by biological vision and object recognition. After preprocessing images, NaturePatternMatch identifies “features” (i.e. spots or other markings) in each of a series of images following Gaussian filters at consecutive spatial scales of analysis that double in size at each step. A vector is assigned to each feature, in which the length corresponds to the feature’s size, and the direction of the vector corresponds to the feature’s orientation. Images can then be compared to each other to determine pairwise similarity, as was done for the eggs of the Common Cuckoo (*Cuculus canorus*) and the various clutches of European species that it parasitizes (Stoddard et al. 2014).

Other methods have been developed to examine pattern regularity, but have seen limited use outside of the studies in which they were conceived. For example, Gluckman and Cardoso (2009) developed a method to estimate the regularity of plumage patterns, such as the bars on the throat of a Peaceful Dove (*Geopelia placida*), in which the proportion of pixels that are black or white in a straightened image are estimated. This method is well-suited to a specific plumage pattern (i.e. bars), and has been used to quantify variation in Common Waxbills (*Estrilda astrild*; Marques et al. 2016), but may not be as widely applicable to quantifying other plumage patterns. Other methods aimed at estimating the “regularity” of patterns have also been developed, such as using fractal geometry to examine associations between individual quality

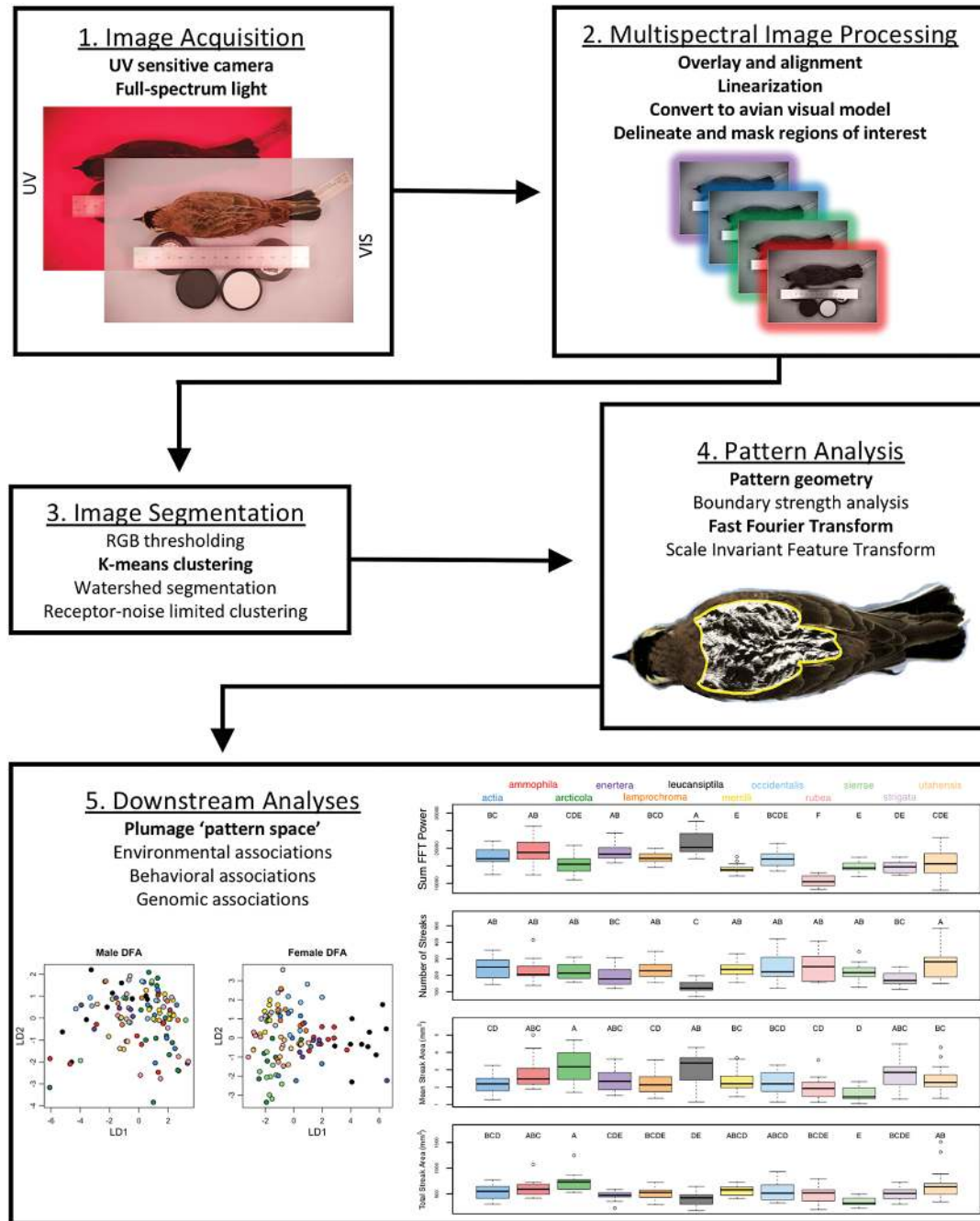


FIGURE 2. Example workflow to quantify plumage patterns. Options for each step are provided below the step heading and the options used in our worked example of Horned Lark (*Eremophila alpestris*) dorsal plumage are shown in bold. Box plots in the downstream analyses figure are for each subspecies with sex included, while the scatterplots on the left show discriminant function analysis scores split by sex with points colored by subspecies. Box plots illustrate variation in sum of the Fast Fourier Transforms at all spatial scales, the number of streaks within the dorsal region of interest, the average size of those streaks, and the total area of streaks within the dorsal region.

and the regularity of bib patterns in Red-legged Partridges (Pérez-Rodríguez et al. 2013). Taken together, methods at estimating pattern regularity are varied, and their effectiveness can be idiosyncratic depending on the spatial and chromatic arrangement of the pattern at hand, but collectively

provide a useful metric that may be related to individual quality (Pérez-Rodríguez et al. 2017).

Collectively, the output of image segmentation and pattern analyses generate an n -dimensional environment that encapsulates phenotypic variation in plumage patterns

across birds that has been coined “pattern space” (Stoddard and Osorio 2019). While ornithologists have studied and measured plumage for centuries, recent developments in the past couple of years have enabled users to collect data in an open-source, user-friendly framework that was previously intractable. Methods such as QCPA (Berg et al. 2020) are scalable in that RAW photographs can be archived and shared among research groups to compile datasets among taxa that would be intractable for lone investigators to accomplish. Future studies can use and build upon these methods to further explore the parameters of avian plumage pattern space and deepen our understanding of the various roles that plumage patterns play in avian biology.

WORKED EXAMPLE: HORNED LARK BACK PATTERNING

Here, we present a worked example on plumage patterning and its quantification among subspecies of the Horned Lark. We present a potential pipeline that could be easily adapted to other studies (Figure 2), but users must take careful consideration to balance an ever-changing array of lighting equipment, cameras, and software to meet their own budgets and other project constraints.

We photographed 14–20 Horned Lark from the western United States that were available as vouchered, round-skin specimens at the Museum of Vertebrate Zoology (Supplemental Material Table S1). We photographed a total of 215 specimens using a Nikon D7000 camera with full-spectrum quartz conversion (Advanced Camera Services Limited, Norfolk, England). We used a Novoflex Noflexar 35 mm lens, which does not filter out UV wavelengths, in combination with a Baader Venus-U filter (~320–380 nm), a Baader UV/IR cut filter (~400–680 nm), and a 3D-printed apparatus to switch between lenses. We included 5% and 80% reflectance standards (Labsphere, North Sutton, New Hampshire, USA) in each photo along with a metric scale bar. All photographs were taken at *f*/3.5, ISO200, in RAW format, with the camera mounted 54 cm above the specimen, using the CaptureOne software suite (PhaseOne, Copenhagen, Denmark). RAW-format photographs are available via the Dryad Data Repository (Mason and Bowie 2020, <https://doi.org/10.6078/D10T3P>).

Digital image processing closely followed the guidelines of Stevens et al. (2007), McKay (2013), and Troscianko and Stevens (2015). We generated normalized multispectral images using the program ImageJ 1.52a (Abràmoff et al. 2004) with the Multispectral Image Calibration and Analysis Toolbox (MICA) 1.22 plugin (Troscianko and Stevens 2015). We aligned UV and visual photos using the auto-align algorithm provided by MICA with offset set to 16 and 2 scaling loops with a scale step size of 0.005. For each image, we drew a freehand polygon corresponding to

the dorsal region of interest (Figure 2). In generating our polygons, we avoided regions of the bird that had feathers missing or were otherwise disturbed during the specimen preparation process. We then converted our stacked UV and RGB image into cone-catch values for the Eurasian Blue Tit (*Cyanistes caeruleus*) visual model, which generates 5 layers: 4 correspond to the UV, short, medium, and long wave length-sensors, and a fifth corresponds to the “double-cone” sensor (Vorobyev et al. 1998). We quantified plumage patterns by performing consecutive FFT algorithms on the polygon of each image from 2 to 128 increasing exponentially by $\sqrt{2}$ and calculated the total power across all transformations for each specimen. We also exported raster layers as TIFFs corresponding to each of the 5 layers of cone-catch values for import into R. We then assigned pixels to 1 of 2 clusters using a *k*-means clustering algorithm on values of the long-wavelength sensor (red cone), which differed the most between dark streaks and background colors for the dorsal regions of lark backs. We then extracted pixels that corresponded to either the light or dark cluster and created polygons from the resulting rasters (Figure 2). From there, we extracted a number of summary statistics, including the number of polygons corresponding to the darker of the 2 clusters (streaks), the sum of the area of darker polygons, the average area of darker polygons, and the standard deviation of the area of darker polygons.

We constructed general linear models for each of the 4 plumage pattern characters with subspecies as the sole main effect. We then performed a Tukey’s honestly significant difference (HSD) test of whether differences in mean values between each pair of subspecies were statistically significant. We also performed a discriminant function analysis on the male and female plumage pattern data separately to examine how well plumage patterns differentiation matched subspecies.

We found differences among subspecies of Horned Lark with respect to dorsal patterning, thereby generating a “plumage pattern space” that could be used to explore associations with other aspects of lark biology, such as phenotype–environment associations (Figure 2). For example, the subspecies *E. a. leucansiptila* had the highest total power across FFTs, suggesting that it had the most “disruptive” plumage patterns on its dorsum. Correspondingly, *E. a. leucansiptila* also had the fewest number of streaks that were on average the largest in area. There is strong reason to believe that dorsal patterning and coloration in *E. alpestris* and other larks is associated with environmental conditions to avoid visual detection by avian predators (Donald et al. 2017, Mason and Unitt 2018). While a thorough quantification of associations with environmental conditions is outside the scope of this review, our case study demonstrates that differences among individuals and populations are quantifiable and represent our ability to

move beyond human categorizations of plumage patterns to more robust quantifications of pattern phenotypes. The methods illustrated here open future avenues of research regarding phenotype–environment–genotype associations in larks and other taxa.

LOOKING AHEAD: THE FUTURE OF PLUMAGE PATTERN RESEARCH

Recent and ongoing conceptual and methodological developments are opening new avenues of research on plumage patterns. We outline 4 possible priorities for future research directions in the context of available resources and time constraints.

First, the advent of new image processing methods have diminished barriers involved in the collection, processing, and analysis of digital photographs and the acquisition of high-quality plumage pattern data. Future studies should move beyond human-based, subjective categorizations of plumage patterns to incorporate open-source, user-friendly quantification pipelines that are based on spatial and chromatic properties of avian vision (e.g., Berg et al. 2020). Many steps of these pipelines can be automated and improved via machine learning, which will unlock large comparative data sets of unprecedented depth and precision. The steps that do require human input are relatively simple and can therefore be crowdsourced (e.g., Drury et al. 2019) or serve as an entry point for new biology students interested in ornithological research (Hiller et al. 2017). Access to comparative databases of high-quality plumage pattern data will enable ornithologists to more accurately infer the various biological roles of plumage patterns at different evolutionary and taxonomic scales, and further expand the growing literature on the macroecology and macroevolution of plumage color (Dale et al. 2015, Dunn et al. 2015, Cooney et al. 2019, Marcondes and Brumfield 2019, Merwin et al. 2020, Price-Waldman et al. 2020). Developing an open-source network to curate and share RAW photographs will ensure that the ornithological community continues to benefit from improving technologies in computer vision and image processing. Sharing photographs in RAW format (the starting point for many image processing pipelines) and the conditions in which those photographs were taken (e.g., which standards were used, camera models) will enable the ornithological community to collectively build large, comparative datasets beyond what a single research group could accomplish, similar to what has been done with genetic data. RAW-format photographs are large files, but data repositories such as Dryad (<https://datadryad.org/>) and Morphosource (<https://www.morphosource.org/>) provide viable options for permanent image storage and data curation.

Second, much of our understanding of how plumage patterns function comes from a small handful of systems

(i.e. Red Junglefowl, Common Quail [*Coturnix coturnix*], Rock Pigeon, House Sparrow, Great Tit, Zebra Finch). These systems have been prioritized because they are tractable, have high-quality genomes, and have extensive existing knowledge from gene annotation and prior eco-evolutionary studies. Yet the ecological functions of plumage patterns inferred from these systems are often assumed to be the same in other taxa. As we have shown here, the roles of plumage patterns vary widely and depend on the evolutionary, environmental, and behavioral context of the system at hand. Future studies should expand their taxonomic scope to incorporate non-model avian taxa that have received less attention at the individual, population, species, and larger clades, thereby enabling a deeper understanding of how plumage patterns contribute to natural history among all species of birds and not just a select few.

Third, as the costs of high-throughput sequencing continue to decrease, we anticipate that genomic data will further elucidate the genetic architecture of plumage patterns. An exciting frontier is to consider the contributions of protein-coding changes to amino acids alongside changes in gene regulation and epigenetics in the diversification of plumage patterns (Ekblom and Galindo 2011, Sepers et al. 2019). For example, population and comparative genomics have shed light on the evolutionary developmental processes driving the evolution of camouflage in mammals and non-avian reptiles (Harris et al. 2019), setting the stage for parallel discoveries in birds. Furthermore, as long-read sequencing technologies continue to improve and more high-quality genome assemblies are made available (e.g., Mason et al. 2020), it will become easier to discern the role that structural DNA variants—such as chromosomal rearrangements and copy number variants—play in the evolutionary development of plumage patterns (Mérot et al. 2020). Even though genome-wide association studies are becoming increasingly common in ornithology, functional validation of candidate loci remains challenging and elusive in birds (Grayson et al. 2017). Nevertheless, we anticipate that discoveries in the “classic” (e.g., chicken, Zebra Finch) and “emerging” (e.g., pigeon, *Ficedula*) model species of birds will illuminate the path for future comparative genomic studies of plumage patterns in non-model avian taxa (Toews et al. 2016a). As the number of candidate loci associated with plumage patterns continues to increase, the field would benefit immensely from additional evolutionary development studies of feathers incorporating different developmental stages and taxa to more accurately understand the functional aspects of genetic and biochemical pathways involved in the dazzling array of plumage patterns seen in birds.

Fourth, color science, material science, and imaging technology have improved dramatically with exciting implications for our understanding of avian coloration and plumage patterns. For example, Fu et al. (2017) combined reflected-light microscopy with digital photography to characterize scattering profiles of butterfly scales, which

could be applied in combination with other methods (e.g., hyperspectral imaging; Harvey et al. 2013) in birds to gain a deeper understanding of the spectral and physical properties underlying variation in structural and iridescent plumage patches and patterns. Additional studies have revealed how feather modifications at the micron scale influence patterns of light scattering and absorption to create “superblack” plumage patches that are taxonomically widespread in birds (McCoy et al. 2018, McCoy and Prum 2019). Improved understanding of feather morphology and the impacts of microscopic variation in feather barbules will further deepen our understanding of how intrafeather patterns and the structural and spectral properties of coloration and patterning among body regions have evolved. Furthermore, combining spectroscopy with digital photography offers a synergistic way to understand spectral and spatial components of avian plumage patterns; sophisticated yet attainable photography setups that combine photography at different angles and wavelengths of light have great potential to generate new insights into how structural and pigment-based plumage patterns differ and evolve. Another ongoing development in computer vision is the application of photogrammetry to museum specimens of birds, by which 3-dimensional models are reconstructed that can be rotated, zoomed, examined, and measured (Medina et al. 2020). The Moore Lab of Zoology has been a leader in this initiative and has already uploaded photogrammetric models for multiple drawers of bird specimens (see <https://sketchfab.com/jmedina2/collections/moore-lab-of-zoology>), enabling users to explore museum holdings and avian biodiversity from anywhere with internet access.

As our ability to document, process, and analyze plumage patterns of museum specimens and live birds continues to improve, we predict exciting discoveries in our understanding of the ecology and evolution of plumage patterns. Large, comprehensive datasets on plumage patterns are more attainable now than ever before, and we stand poised to deepen our understanding of their role in avian biology and diversification. Plumage patterns have inspired and amazed ornithologists for centuries and will continue to do so long into the future.

SUPPLEMENTAL MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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Data depository: Analyses reported in this article can be reproduced using the data provided by Mason and Bowie (2020).

LITERATURE CITED

- Abolins-Abols, M., E. Kornobis, P. Ribeca, K. Wakamatsu, M. P. Peterson, E. D. Ketterson, and B. Milá (2018). Differential gene regulation underlies variation in melanic plumage coloration in the Dark-eyed Junco (*Junco hyemalis*). *Molecular Ecology* 27:4501–4515.
- Abramoff, D. M. D., P. Magelhaes, and S. Ram (2004). Image processing with ImageJ. *Biophotonics International* 11:36–42.
- Álvarez, F. (2004). Black and white tail markings in Rufous Bush Chats *Cercotrichas galactotes*: Size, symmetry and the extent of seasonal abrasion. *Ardeola* 51:169–175.
- Andersen, M. J., Á. S. Nyári, I. Mason, L. Joseph, J. P. Dumbacher, C. E. Filardi, and R. G. Moyle (2014). Molecular systematics of the world's most polytypic bird: The *Pachycephala pectoralis/melanura* (Aves: Pachycephalidae) species complex. *Zoological Journal of the Linnean Society* 170:566–588.
- Arifin, A. Z., and A. Asano (2006). Image segmentation by histogram thresholding using hierarchical cluster analysis. *Pattern Recognition Letters* 27:1515–1521.
- Badyaev, A. V., G. E. Hill, P. O. Dunn, and J. C. Glen (2001). Plumage color as a composite trait: Developmental and functional integration of sexual ornamentation. *The American Naturalist* 158:221–235.
- Badyaev, A. V., E. S. Morrison, V. Belloni, and M. J. Sanderson (2015). Tradeoff between robustness and elaboration in carotenoid networks produces cycles of avian color diversification. *Biology Direct* 10:45.
- Baião, P. C., and P. G. Parker (2012). Evolution of the melanocortin-1 receptor (MC1R) in boobies and gannets (Aves, Suliformes). *Journal of Heredity* 103:322–329.
- Baiz, M. D., G. R. Kramer, H. M. Streby, S. A. Taylor, I. J. Lovette, and D. P. L. Toews (2020). Genomic and plumage variation in *Vermivora* hybrids. *The Auk: Ornithological Advances* 137:1–14. doi:10.1093/auk/ukaa027.
- Beer, C. G. (1971). Individual recognition of voice in the social behavior of birds. *Advances in the Study of Behavior* 3:27–74.
- Berg, C. P., J. Troschianko, J. A. Endler, N. J. Marshall, and K. L. Cheney (2020). Quantitative Colour Pattern Analysis

- (QCPA): A comprehensive framework for the analysis of colour patterns in nature. *Methods in Ecology and Evolution* 11:316–332.
- Beucher, S. (1991). The watershed transformation applied to image segmentation. In *Proceedings of the 10th Pfefferkorn Conference on Signal and Image Processing in Microscopy and Microanalysis*, Cambridge, UK, 1992. pp. 299–314.
- Blizard, M., and S. Pruett-Jones (2017). Plumage pattern dimorphism in a shorebird exhibiting sex-role reversal (*Actitis macularius*). *The Auk: Ornithological Advances* 134:363–376.
- Booth, C. L. (1990). Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* 40:125–163.
- Bortolotti, G. R., J. Blas, J. J. Negro, and J. L. Tella (2006). A complex plumage pattern as an honest social signal. *Animal Behaviour* 72:423–430.
- Bourgeois, Y. X., J. A. Bertrand, C. Thébaud, and B. Milá (2012). Investigating the role of the melanocortin-1 receptor gene in an extreme case of microgeographical variation in the pattern of melanin-based plumage pigmentation. *PLOS One* 7:e50906.
- Brelsford, A., D. P. L. Toews, and D. E. Irwin (2017). Admixture mapping in a hybrid zone reveals loci associated with avian feather coloration. *Proceedings of the Royal Society B* 284:20171106.
- Bretagnolle, V., J.-C. Thibault, and J.-M. Dominici (1994). Field identification of individual Ospreys using head marking pattern. *The Journal of Wildlife Management* 58:175–178.
- Brodie, E. D., III. (1992). Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* 46:1284–1298.
- Bruders, R., H. Van Hollebeke, E. J. Osborne, Z. Kronenberg, E. Maclary, M. Yandell, and M. D. Shapiro (2020). A copy number variant is associated with a spectrum of pigmentation patterns in the Rock Pigeon (*Columba livia*). *Plos Genetics* 16:e1008274.
- Budden, A. E., and J. L. Dickinson (2009). Signals of quality and age: The information content of multiple plumage ornaments in male Western Bluebirds *Sialia mexicana*. *Journal of Avian Biology* 40:18–27.
- Burns, K. J. (1998). A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): The role of female versus male plumage. *Evolution* 52:1219–1224.
- Burns, K. J., and A. J. Shultz (2012). Widespread cryptic dichromatism and ultraviolet reflectance in the largest radiation of Neotropical songbirds: Implications of accounting for avian vision in the study of plumage evolution. *The Auk* 129:211–221.
- Burns, K. J., K. J. McGraw, A. J. Shultz, M. C. Stoddard, and D. B. Thomas (2017). Advanced methods for studying pigments and coloration using avian specimens. In *The Extended Specimen: Emerging Frontiers in Collections-Based Ornithological Research* (M. W. Webster, Editor). CRC Press, Boca Raton, FL, USA. pp. 23–55.
- Burt, E. H. (1981). The adaptiveness of animal colors. *BioScience* 31:723–729.
- Butcher, G., and S. Rohwer (1989). The evolution of conspicuous and distinctive coloration for communication in birds. *Current Ornithology* 6:51–108.
- Campagna, L., M. Repenning, L. F. Silveira, C. S. Fontana, P. L. Tubaro, and I. J. Lovette (2017). Repeated divergent selection on pigmentation genes in a rapid finch radiation. *Science Advances* 3:e1602404.
- Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience* 55:125.
- Caro, T., and W. L. Allen (2017). Interspecific visual signalling in animals and plants: A functional classification. *Philosophical Transactions of the Royal Society B* 372:20160344.
- Cermak, T., E. L. Doyle, M. Christian, L. Wang, Y. Zhang, C. Schmidt, J. A. Baller, N. V. Somia, A. J. Bogdanove, and D. F. Voytas (2011). Efficient design and assembly of custom TALEN and other TAL effector-based constructs for DNA targeting. *Nucleic Acids Research* 39:e82.
- Chaine, A. S., K. A. Tjernell, D. Shizuka, and B. E. Lyon (2011). Sparrows use multiple status signals in winter social flocks. *Animal Behaviour* 81:447–453.
- Chan, I. Z. W., M. Stevens, and P. A. Todd (2019). PAT-GEOM: A software package for the analysis of animal patterns. *Methods in Ecology and Evolution* 10:591–600.
- Chen, C. F., J. Foley, P. C. Tang, A. Li, T. X. Jiang, P. Wu, R. B. Wideltz, and C. M. Chuong (2015). Development, regeneration, and evolution of feathers. *Annual Review of Animal Biosciences* 3:169–195.
- Cheviron, Z. A., S. J. Hackett, and R. T. Brumfield (2006). Sequence variation in the coding region of the melanocortin-1 receptor gene (*MC1R*) is not associated with plumage variation in the Blue-crowned Manakin (*Lepidothrix coronata*). *Proceedings of the Royal Society B* 273:1613–1618.
- Christin, S., É. Hervet, and N. Lecomte (2019). Applications for deep learning in ecology. *Methods in Ecology and Evolution* 10:1632–1644.
- Cibois, A., J.-C. Thibault, and E. Pasquet (2012). The molecular basis of the plumage colour polymorphism in the Tahiti Reed-Warbler *Acrocephalus caffer*. *Journal of Avian Biology* 43:3–8.
- Cicero, C., N. A. Mason, L. Benedict, and J. D. Rising (2020). Behavioral, morphological, and ecological trait evolution in two clades of New World Sparrows (*Aimophila* and *Peucaea*, Passerellidae). *PeerJ* 8:e9249.
- Clark, W. S., and P. Pyle (2015). A recommendation for standardized age-class plumage terminology for raptors. *Journal of Raptor Research* 49:513–517.
- Cooke, T. F., C. R. Fischer, P. Wu, T. X. Jiang, K. T. Xie, J. Kuo, E. Doctorov, A. Zehnder, C. Khosla, C. M. Chuong, and C. D. Bustamante (2017). Genetic mapping and biochemical basis of yellow feather pigmentation in Budgerigars. *Cell* 171:427–439.
- Cooney, C. R., Z. K. Varley, L. O. Nouri, C. J. A. Moody, M. D. Jardine, and G. H. Thomas (2019). Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications* 10:1773.
- Cooper, C. A., T. J. Doran, A. Challagulla, M. L. V. Tizard, and K. A. Jenkins (2018). Innovative approaches to genome editing in avian species. *Journal of Animal Science and Biotechnology* 9:15.
- Cordero, P. J., J. H. Wetton, and D. T. Parkin (1999). Extra-pair paternity and male badge size in the House Sparrow. *Journal of Avian Biology* 30:97–102.
- Cott, H. (1940). *Adaptive Coloration in Animals*. Methuen, London, UK.

- Cowles, S. A., and J. A. C. Uy (2019). Rapid, complete reproductive isolation in two closely related *Zosterops* white-eye bird species despite broadly overlapping ranges. *Evolution* 73:1647–1662.
- Cuthill, I. C., W. L. Allen, K. Arbuckle, B. Caspers, G. Chaplin, M. E. Hauber, G. E. Hill, N. G. Jablonski, C. D. Jiggins, A. Kelber, et al. (2017). The biology of color. *Science* 357:eaan0221.
- Cuthill, I. C., M. Stevens, J. Sheppard, T. Maddocks, C. A. Párraga, and T. S. Troscianko (2005). Disruptive coloration and background pattern matching. *Nature* 434:72–74.
- Dale, J. (2006). Intraspecific variation in coloration. In *Bird Coloration: Function and Evolution* (G. Hill and K. McGraw, Editors). Harvard University Press, Cambridge, MA, USA.
- Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature* 527:367–370.
- Dale, S., and T. Slagsvold (1996). Plumage coloration and conspicuousness in birds: Experiments with the Pied Flycatcher. *The Auk* 113:849–857.
- Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. Murray, London, UK.
- Delmore, K. E., D. P. Toews, R. R. Germain, G. L. Owens, and D. E. Irwin (2016). The genetics of seasonal migration and plumage color. *Current Biology* 26:2167–2173.
- Deppe, C., D. Holt, J. Tewksbury, L. Broberg, J. Petersen, and K. Wood (2003). Effect of Northern Pygmy-Owl (*Glaucidium gnoma*) eyespots on avian mobbing. *The Auk* 120:765–771.
- Dobson, A. E., D. J. Schmidt, and J. M. Hughes (2012). Sequence variation in the melanocortin-1 receptor (MC1R) does not explain continent-wide plumage color differences in the Australian Magpie (*Cracticus tibicen*). *The Journal of Heredity* 103:769–780.
- Domingos, P., and M. Pazzani (1997). On the optimality of the simple Bayesian classifier under zero-one loss. *Machine Learning* 29:103–130.
- Domingues, V. S., Y. P. Poh, B. K. Peterson, P. S. Pennings, J. D. Jensen, and H. E. Hoekstra (2012). Evidence of adaptation from ancestral variation in young populations of beach mice. *Evolution* 66:3209–3223.
- Donald, P. F., P. Alström, and D. Engelbrecht (2017). Possible mechanisms of substrate colour-matching in larks (Alaudidae) and their taxonomic implications. *Ibis* 159:699–702.
- Doudna, J. A., and E. Charpentier (2014). Genome editing. The new frontier of genome engineering with CRISPR-Cas9. *Science* 346:1258096.
- Drury, J. P., M. Barnes, A. E. Finneran, M. Harris, and G. F. Grether (2019). Continent-scale phenotype mapping using citizen scientists' photographs. *Ecography* 42:1436–1445.
- Dumbacher, J. P., and R. C. Fleischer (2001). Phylogenetic evidence for colour pattern convergence in toxic *Pitohuis*: Müllerian mimicry in birds? *Proceedings of the Royal Society of London, Series B* 268:1971–1976.
- Dumbacher, J. P., K. Deiner, L. Thompson, and R. C. Fleischer (2008). Phylogeny of the avian genus *Pitohui* and the evolution of toxicity in birds. *Molecular Phylogenetics and Evolution* 49:774–781.
- Dunn, P. O., J. K. Armenta, and L. A. Whittingham (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Science Advances* 1:e1400155.
- Dunn, P. O., J. C. Garvin, L. A. Whittingham, C. R. Freeman-Gallant, and D. Hasselquist (2010). Carotenoid and melanin-based ornaments signal similar aspects of male quality in two populations of the Common Yellowthroat. *Functional Ecology* 24:149–158.
- Duyck, J., C. Finn, A. Hutcheon, P. Vera, J. Salas, and S. Ravela (2015). Sloop: A pattern retrieval engine for individual animal identification. *Pattern Recognition* 48:1059–1073.
- Dwight, J. (1925). The gulls (Laridae) of the world: Their plumages, molt variations, relationship and distribution. *Bulletin of the American Museum of Natural History* 52:1–401.
- Dyck, J. (1985). The evolution of feathers. *Zoologica Scripta* 14:137–154.
- Eaton, M. D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *Proceedings of the National Academy of Sciences USA* 102:10942–10946.
- Eklom, R., and J. Galindo (2011). Applications of next generation sequencing in molecular ecology of non-model organisms. *Heredity* 107:1–15.
- Eliason, C. M., M. J. Andersen, and S. J. Hackett (2019). Using historical biogeography models to study color pattern evolution. *Systematic Biology* 68:755–766.
- Endler, J. A. (1978). A predator's view of animal color patterns. In *Evolutionary Biology* (M. K. Hecht, W. C. Steere, and B. Wallace, Editors). Springer, Boston, MA, USA. pp. 319–364.
- Endler, J. A. (1990). On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41:315–352.
- Endler, J. A. (1991). Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research* 31:587–608.
- Endler, J. A. (2012). A framework for analysing colour pattern geometry: Adjacent colours. *Biological Journal of the Linnean Society* 107:233–253.
- Endler, J. A., and P. W. Mielke (2005). Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society* 86:405–431.
- Endler, J. A., G. L. Cole, and A. M. Kranz (2018). Boundary strength analysis: Combining colour pattern geometry and coloured patch visual properties for use in predicting behaviour and fitness. *Methods in Ecology and Evolution* 9:2334–2348.
- Figuerola, J., and J. C. Senar (2000). Measurement of plumage badges: An evaluation of methods used in the Great Tit *Parus major*. *Ibis* 142:482–484.
- Frith, C. (1978). The function of display and coloration in the Sunbittern. *Avicultural Magazine* 84:150–157.
- Fu, J., B. J. Yoon, J. O. Park, and M. Srinivasarao (2017). Imaging optical scattering of butterfly wing scales with a microscope. *Interface Focus* 7:20170016.
- Funk, E. R., and S. A. Taylor (2019). High-throughput sequencing is revealing genetic associations with avian plumage color. *The Auk: Ornithological Advances* 136:1–7. <https://doi.org/10.1093/auk/ukz048>
- Galeotti, P., D. Rubolini, P. O. Dunn, and M. Fasola (2003). Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology* 16:635–646.
- Galván, I., and J. J. Sanz (2008). The cheek plumage patch is an amplifier of dominance in Great Tits. *Biology Letters* 4:12–15.
- Galván, I., and F. Solano. (2016). Bird integumentary melanins: Biosynthesis, forms, function and evolution. *International Journal of Molecular Sciences* 17:520.
- Galván, I., J. García-Campa, and J. J. Negro (2017). Complex plumage patterns can be produced only with the contribution

- of melanins. *Physiological and Biochemical Zoology* 90:600–604.
- Gangoso, L., J. M. Grande, A. L. Ducrest, J. Figuerola, G. R. Bortolotti, J. A. Andrés, and A. Roulin (2011). MC1R-dependent, melanin-based colour polymorphism is associated with cell-mediated response in the Eleonora's Falcon. *Journal of Evolutionary Biology* 24:2055–2063.
- Garamszegi, L. Z., B. Rosivall, G. Hegyi, E. Szöllösi, J. Török, and M. Eens (2006). Determinants of male territorial behavior in a Hungarian Collared Flycatcher population: Plumage traits of residents and challengers. *Behavioral Ecology and Sociobiology* 60:663–671.
- Garg, K. M., K. Sam, B. Chattopadhyay, K. R. Sadanandan, B. Koane, P. G. P. Ericson, and F. E. Rheindt (2019). Gene flow in the Müllerian mimicry ring of a poisonous Papuan songbird clade (*Pitohui*; Aves). *Genome Biology and Evolution* 11:2332–2343.
- Gluckman, T.-L., and G. C. Cardoso (2009). A method to quantify the regularity of barred plumage patterns. *Behavioral Ecology and Sociobiology* 63:1837–1844.
- Gluckman, T. L., and G. C. Cardoso. (2010). The dual function of barred plumage in birds: Camouflage and communication. *Journal of Evolutionary Biology* 23:2501–2506.
- Gluckman, T.-L., and N. I. Mundy (2013). Cuckoos in raptors' clothing: Barred plumage illuminates a fundamental principle of Batesian mimicry. *Animal Behaviour* 86:1165–1181.
- Gluckman, T.-L., and N. I. Mundy (2016). Evolutionary pathways to convergence in plumage patterns. *BMC Evolutionary Biology* 16:172.
- Godfrey, D., J. N. Lythgoe, and D. A. Rumball (1987). Zebra stripes and tiger stripes: The spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biological Journal of the Linnean Society* 32:427–433.
- Gomez, D., and M. Théry (2004). Influence of ambient light on the evolution of colour signals: Comparative analysis of a Neotropical rainforest bird community: Ambient light influences colour evolution. *Ecology Letters* 7:279–284.
- Gómez, J., C. Ramo, J. Troschianko, M. Stevens, M. Castro, A. Pérez-Hurtado, G. Liñán-Cembrano, and J. A. Amat (2018). Individual egg camouflage is influenced by microhabitat selection and use of nest materials in ground-nesting birds. *Behavioral Ecology and Sociobiology* 72:142.
- Gonzalez, G., G. Sorci, A. P. Moller, P. Ninni, C. Haussy, and F. De Lope (1999). Immunocompetence and condition-dependent sexual advertisement in male House Sparrows (*Passer domesticus*). *Journal of Animal Ecology* 68:1225–1234.
- Grant, P. R. (1986). *Gulls: A Guide to Identification*. Buteo Books, Arrington, VA, USA.
- Grayson, P., S. Y. W. Sin, T. B. Sackton, and S. V. Edwards (2017). Comparative genomics as a foundation for evo-devo studies in birds. *Methods in Molecular Biology* 1650:11–46.
- Griggio, M., L. Serra, D. Licheri, A. Monti, and A. Pilastro (2006). Armaments and ornaments in the Rock Sparrow: A possible dual utility of a carotenoid-based feather signal. *Behavioral Ecology and Sociobiology* 61:423–433.
- Harris, R. B., K. Irwin, M. R. Jones, S. Laurent, R. D. H. Barrett, M. W. Nachman, J. M. Good, C. R. Linnen, J. D. Jensen, and S. P. Pfeifer (2019). The population genetics of crypsis in vertebrates: Recent insights from mice, hares, and lizards. *Heredity* 124:1–14.
- Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research* 20:675–703.
- Hartigan, J. A., and M. A. Wong (1979). Algorithm AS 136: A K-means clustering algorithm. *Applied Statistics* 28:100.
- Harvey, T. A., K. S. Bostwick, and S. Marschner (2013). Directional reflectance and milli-scale feather morphology of the African Emerald Cuckoo, *Chrysococcyx cupreus*. *Journal of the Royal Society Interface* 10:20130391.
- Haupaix, N., and M. Manceau (2019). The embryonic origin of periodic color patterns. *Developmental Biology* 460:70–76.
- Haupaix, N., C. Curantz, R. Bailleul, S. Beck, A. Robic, and M. Manceau (2018). The periodic coloration in birds forms through a prepattern of somite origin. *Science* 361:eaar4777.
- Hill, G. E. (1999). Pairing success relative to male plumage redness and pigment symmetry in the House Finch: Temporal and geographic constancy. *Behavioral Ecology* 10:48–53.
- Hill, G. E. (2006). Female mate choice for ornamental coloration. In *Bird Coloration: Function, and Evolution*, vol. 2 (G. E. Hill and K. McGraw, Editors). Harvard University Press, London, UK.
- Hill, G. E., and K. J. McGraw (2006). *Bird Coloration: Function and Evolution*. Harvard University Press, London, UK.
- Hiller, A. E., C. Cicero, M. J. Albe, T. L. W. Barclay, C. L. Spencer, M. S. Koo, R. C. K. Bowie, and E. A. Lacey (2017). Mutualism in museums: A model for engaging undergraduates in biodiversity science. *Plos Biology* 15:e2003318.
- Hoekstra, H. E., R. J. Hirschmann, R. A. Bunday, P. A. Insel, and J. P. Crossland (2006). A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science* 313:101–104.
- Hofmann, C. M., T. W. Cronin, and K. E. Omland (2008). Evolution of sexual dichromatism. 1. Convergent losses of elaborate female coloration in New World orioles (*Icterus* spp.). *The Auk* 125:778–789.
- Hogan-Warburg, A. J. (2002). Social behavior of the Ruff, *Philomachus pugnax* (L.). *Ardea* 54:109–229.
- Hogstad, O., and R. T. Kroglund (1993). The throat badge as a status signal in juvenile male Willow Tits *Parus montanus*. *Journal of Ornithology* 134:413–423.
- Howell, S. (2010). *Molt in North American Birds*. Houghton Mifflin Harcourt, Boston, MA, USA.
- Hubbard, J. K., J. A. Uy, M. E. Hauber, H. E. Hoekstra, and R. J. Safran (2010). Vertebrate pigmentation: From underlying genes to adaptive function. *Trends in Genetics* 26:231–239.
- Hudson, E. J., and T. D. Price (2014). Pervasive reinforcement and the role of sexual selection in biological speciation. *The Journal of Heredity* 105 Suppl 1:821–833.
- Humphrey, P. S., and K. C. Parkes (1959). An approach to the study of molts and plumages. *The Auk* 76:1–31.
- Huynh, L. Y., D. L. Maney, and J. W. Thomas (2011). Chromosome-wide linkage disequilibrium caused by an inversion polymorphism in the White-throated Sparrow (*Zonotrichia albicollis*). *Heredity* 106:537–546.
- Janicke, T., M. G. Ritchie, E. H. Morrow, and L. Marie-Orleach (2018). Sexual selection predicts species richness across the animal kingdom. *Proceedings of the Royal Society B* 285:20180173.

- Järvi, T., and M. Bakken (1984). The function of the variation in the breast stripe of the Great Tit (*Parus major*). *Animal Behaviour* 32:590–596.
- Jawor, J. M., and R. Breitwisch (2003). Melanin ornaments, honesty, and sexual selection. *The Auk* 120:249–265.
- Jiang, T. X., R. B. Wideltz, W. M. Shen, P. Will, D. Y. Wu, C. M. Lin, H. S. Jung, and C. M. Chuong (2004). Integument pattern formation involves genetic and epigenetic controls: Feather arrays simulated by digital hormone models. *The International Journal of Developmental Biology* 48:117–135.
- Jiguet, F., and V. Bretagnolle (2014). Sexy males and choosy females on exploded leks: Correlates of male attractiveness in the Little Bustard. *Behavioural Processes* 103:246–255.
- Johnson, N. K. (1972). Origin and differentiation of the avifauna of the Channel Islands, California. *The Condor* 74:295–315.
- Johnstone, R. A., and K. Norris (1993). Badges of status and the cost of aggression. *Behavioral Ecology and Sociobiology* 32:127–134.
- Jönsson, K. A., R. C. K. Bowie, J. A. Norman, L. Christidis, and J. Fjeldså (2008). Polyphyletic origin of toxic *Pitohui* birds suggests widespread occurrence of toxicity in corvid birds. *Biology Letters* 4:71–74.
- Jönsson, K. A., K. Delhey, G. Sangster, P. G. P. Ericson, and M. Irestedt (2016). The evolution of mimicry of friarbirds by orioles (Aves: Passeriformes) in Australo-Pacific archipelagos. *Proceedings of the Royal Society B* 283:20160409.
- Joron, M., and J. L. Mallet (1998). Diversity in mimicry: Paradox or paradigm? *Trends in Ecology & Evolution* 13:461–466.
- Jouventin, P., P. M. Nolan, F. S. Dobson, and M. Nicolaus (2008). Coloured patches influence pairing rate in King Penguins. *Ibis* 150:193–196.
- Kearns, A. M., L. Joseph, J. J. Austin, A. C. Driskell, and K. E. Omland (2020). Complex mosaic of sexual dichromatism and monochromatism in Pacific Robins results from both gains and losses of elaborate coloration. *Journal of Avian Biology* 51:jav.02404.
- Kim, K. W., B. C. Jackson, H. Zhang, D. P. L. Toews, S. A. Taylor, E. I. Greig, I. J. Lovette, M. M. Liu, A. Davison, S. C. Griffith, K. Zeng, and T. Burke (2019). Genetics and evidence for balancing selection of a sex-linked colour polymorphism in a songbird. *Nature Communications* 10:1852.
- Kokko, H. (1997). Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41:99–107.
- Kondo, S. (2002). The reaction–diffusion system: A mechanism for autonomous pattern formation in the animal skin. *Genes to Cells* 7:535–541.
- Kondo, S., and T. Miura (2010). Reaction–diffusion model as a framework for understanding biological pattern formation. *Science* 329:1616–1620.
- Kornilov, A., and I. Safonov (2018). An overview of watershed algorithm implementations in open source libraries. *Journal of Imaging* 4:123.
- Kose, M., and A. P. Møller (1999). Sexual selection, feather breakage and parasites: The importance of white spots in the tail of the Barn Swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology* 45:430–436.
- Kraaijeveld, K., F. J. Kraaijeveld-Smit, and M. E. Maan (2011). Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews of the Cambridge Philosophical Society* 86:367–377.
- Krebs, J. R., and D. E. Kroodsma (1980). Repertoires and geographical variation in bird song. *Advances in the Study of Behavior* 11:143–177.
- Kühl, H. S., and T. Burghardt (2013). Animal biometrics: Quantifying and detecting phenotypic appearance. *Trends in Ecology & Evolution* 28:432–441.
- Küpper, C., M. Stocks, J. E. Risse, N. Dos Remedios, L. L. Farrell, S. B. McRae, T. C. Morgan, N. Karlionova, P. Pinchuk, Y. I. Verkuil, et al. (2016). A supergene determines highly divergent male reproductive morphs in the Ruff. *Nature Genetics* 48:79–83.
- Lamichhaney, S., G. Fan, F. Widemo, U. Gunnarsson, D. S. Thalmann, M. P. Hoepfner, S. Kerje, U. Gustafson, C. Shi, H. Zhang, et al. (2016). Structural genomic changes underlie alternative reproductive strategies in the Ruff (*Philomachus pugnax*). *Nature Genetics* 48:84–88.
- Lank, D. B. (2002). Diverse processes maintain plumage polymorphisms in birds. *Journal of Avian Biology* 33:327–330.
- Lank, D. B., and J. Dale (2001). Visual signals for individual identification: The silent “song” of Ruffs. *The Auk* 118:759–765.
- Laucht, S., B. Kempenaers, and J. Dale (2010). Bill color, not badge size, indicates testosterone-related information in House Sparrows. *Behavioral Ecology and Sociobiology* 64:1461–1471.
- Lawton, M., and R. Lawton (1985). Heterochrony, deferred breeding, and avian sociality. *Current Ornithology* 3:187–222.
- Leighton, G. M., A. C. Lees, and E. T. Miller (2018). The hairy-downy game revisited: An empirical test of the interspecific social dominance mimicry hypothesis. *Animal Behaviour* 137:141–148.
- Leung, B., and M. R. Forbes (1996). Fluctuating asymmetry in relation to stress and fitness: Effects of trait type as revealed by meta-analysis. *Ecoscience* 3:400–413.
- Li, Q., K. Q. Gao, J. Vinther, M. D. Shawkey, J. A. Clarke, L. D’Alba, Q. Meng, D. E. Briggs, and R. O. Prum (2010). Plumage color patterns of an extinct dinosaur. *Science* 327:1369–1372.
- Liang, W., and A. P. Møller (2015). Hawk mimicry in cuckoos and anti-parasitic aggressive behavior of Barn Swallows in Denmark and China. *Journal of Avian Biology* 46:216–223.
- Ligon, R. A., C. D. Diaz, J. L. Morano, J. Troscianko, M. Stevens, A. Moskeland, T. G. Laman, and E. Scholes III (2018). Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *Plos Biology* 16:e2006962.
- Ligon, R. A., R. K. Simpson, N. A. Mason, G. E. Hill, and K. J. McGraw (2016). Evolutionary innovation and diversification of carotenoid-based pigmentation in finches. *Evolution* 70:2839–2852.
- Liker, A., and Z. Barta (2001). Male badge size predicts dominance against females in House Sparrows. *The Condor* 103:151–157.
- Lopes, L. E., A. V. Chaves, M. M. de Aquino, L. F. Silveira, and F. R. dos Santos (2018). The striking polyphyly of *Suiriri*: Convergent evolution and social mimicry in two cryptic Neotropical birds. *Journal of Zoological Systematics and Evolutionary Research* 56:270–279.
- Lopes, R. J., J. D. Johnson, M. B. Toomey, M. S. Ferreira, P. M. Araujo, J. Melo-Ferreira, L. Andersson, G. E. Hill, J. C. Corbo, and M. Carneiro (2016). Genetic basis for red coloration in birds. *Current Biology* 26:1427–1434.
- Lowe, D. G. (1999). Object recognition from local scale-invariant features. In *Proceedings of the Seventh IEEE International*

- Conference on Computer Vision, vol. 2. IEEE, Kerkyra, Greece. pp. 1150–1157.
- MacDougall-Shackleton, E. A., L. Blanchard, S. A. Igdoura, and H. L. Gibbs (2003). Unmelanized plumage patterns in Old World leaf warblers do not correspond to sequence variation at the melanocortin-1 receptor locus (MC1R). *Molecular Biology and Evolution* 20:1675–1681.
- Maia, R., H. Gruson, J. A. Endler, and T. E. White (2019). PAVO 2: New tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* 10:1097–1107.
- Maia, R., D. R. Rubenstein, and M. D. Shawkey (2013). Key ornamental innovations facilitate diversification in an avian radiation. *Proceedings of the National Academy of Sciences USA* 110:10687–10692.
- Maia, R., D. R. Rubenstein, and M. D. Shawkey (2016). Selection, constraint, and the evolution of coloration in African starlings. *Evolution* 70:1064–1079.
- Malcom, S. B. (1990). Mimicry: Status of a classical evolutionary paradigm. *Trends in Ecology & Evolution* 5:57–62.
- Mammen, D. L., and S. Nowicki (1981). Individual differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology* 9:179–186.
- Manceau, M., V. S. Domingues, C. R. Linnen, E. B. Rosenblum, and H. E. Hoekstra (2010). Convergence in pigmentation at multiple levels: Mutations, genes and function. *Philosophical Transactions of the Royal Society of London, Series B* 365:2439–2450.
- Mappes, J., N. Marples, and J. A. Endler (2005). The complex business of survival by aposematism. *Trends in Ecology & Evolution* 20:598–603.
- Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362:149–152.
- Marchetti, K. (1998). The evolution of multiple male traits in the Yellow-browed Leaf Warbler. *Animal Behaviour* 55:361–376.
- Marcondes, R. S., and R. T. Brumfield (2019). Fifty shades of brown: Macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. *Evolution* 73:704–719.
- Marques, C. I., H. R. Batalha, and G. C. Cardoso (2016). Signalling with a cryptic trait: The regularity of barred plumage in Common Waxbills. *Royal Society Open Science* 3:160195.
- Marshall, K. L., and T. L. Gluckman (2015). The evolution of pattern camouflage strategies in waterfowl and game birds. *Ecology and Evolution* 5:1981–1991.
- Martin, P. R., R. Montgomerie, and S. C. Loughheed (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *The American Naturalist* 185:443–451.
- Masello, J. F., and P. Quillfeldt (2003). Body size, body condition and ornamental feathers of Burrowing Parrots: Variation between years and sexes, assortative mating and influences on breeding success. *Emu - Austral Ornithology* 103:149–161.
- Mason, N. A., and R. C. K. Bowie (2020). Data from: Plumage patterns: Ecological functions, evolutionary origins, and advances in quantification. *The Auk: Ornithological Advances* 137:1–29. <https://doi.org/10.6078/D10T3P>
- Mason, N. A., and S. A. Taylor (2015). Differentially expressed genes match bill morphology and plumage despite largely undifferentiated genomes in a Holarctic songbird. *Molecular Ecology* 24:3009–3025.
- Mason, N. A., and P. Unitt (2018). Rapid phenotypic change in a native bird population following conversion of the Colorado Desert to agriculture. *Journal of Avian Biology* 49:jav-01507.
- Mason, N. A., P. Pulgarin, C. D. Cadena, and I. J. Lovette (2020). De novo assembly of a high-quality reference genome for the Horned Lark (*Eremophila alpestris*). G3: Genes, Genomes, Genetics 10:475–478.
- Mason, N. A., A. J. Shultz, and K. J. Burns (2014). Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. *Proceedings of the Royal Society B* 281:20140967.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia University Press, New York, NY, USA.
- McCoy, D. E., and R. O. Prum (2019). Convergent evolution of super black plumage near bright color in 15 bird families. *The Journal of Experimental Biology* 222:jeb208140.
- McCoy, D. E., T. Feo, T. A. Harvey, and R. O. Prum (2018). Structural absorption by barbule microstructures of super black bird of paradise feathers. *Nature Communications* 9:1.
- McGarigal, K., and B. J. Marks (1995). FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. USDA Forest Service PNW-GTR-351.
- McGlothlin, J. W., D. L. Duffy, J. L. Henry-Freeman, and E. D. Ketterson (2007). Diet quality affects an attractive white plumage pattern in Dark-eyed Juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology* 61:1391–1399.
- McGraw, K. (2006). Mechanics of uncommon colors: Pterins, porphyrins, and psittacofulvins. In *Bird Coloration: Mechanisms and Measurements* (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, Cambridge, MA, USA. pp. 354–398.
- McGraw, K. J. (2008). An update on the honesty of melanin-based color signals in birds. *Pigment Cell & Melanoma Research* 21:133–138.
- McGraw, K. J., and G. E. Hill (2000). Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London B* 267:1525–1531.
- McGraw, K. J., G. E. Hill, and R. S. Parker (2003). Carotenoid pigments in a mutant cardinal: Implications for the genetic and enzymatic control mechanisms of carotenoid metabolism in birds. *The Condor* 105:587–592.
- McGraw, K. J., E. A. Mackillop, J. Dale, and M. E. Hauber (2002). Different colors reveal different information: How nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *The Journal of Experimental Biology* 205:3747–3755.
- McKay, B. D. (2013). The use of digital photography in systematics. *Biological Journal of the Linnean Society* 110:1–13.
- McNaught, M. K., and I. P. F. Owens (2002). Interspecific variation in plumage colour among birds: Species recognition or light environment? *Journal of Evolutionary Biology* 15:505–514.
- Medina, J. J., J. M. Maley, S. Sannapareddy, N. N. Medina, C. M. Gilman, and J. E. McCormack (2020). A rapid and cost-effective pipeline for digitization of museum specimens with 3D photogrammetry. *PLoS One* 15:e0236417.
- Mérot, C., R. A. Oomen, A. Tigano, and M. Wellenreuther (2020). A roadmap for understanding the evolutionary significance

- of structural genomic variation. *Trends in Ecology & Evolution* 35:561–572.
- Merwin, J. T., G. F. Seeholzer, and B. T. Smith (2020). Macroevolutionary bursts and constraints generate a rainbow in a clade of tropical birds. *BMC Evolutionary Biology* 20:32.
- Miao, Z., K. M. Gaynor, J. Wang, Z. Liu, O. Muellerklein, M. S. Norouzzadeh, A. McInturff, R. C. K. Bowie, R. Nathan, S. X. Yu, and W. M. Getz (2019). Insights and approaches using deep learning to classify wildlife. *Scientific Reports* 9:8137.
- Miller, A. H., and L. Miller (1951). Geographic variation of the Screech Owls of the deserts of western North America. *The Condor* 53:161–177.
- Miller, E. T., G. M. Leighton, B. G. Freeman, A. C. Lees, and R. A. Ligon (2019). Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. *Nature Communications* 10:1602.
- Mills, M. G., and L. B. Patterson (2009). Not just black and white: Pigment pattern development and evolution in vertebrates. *Seminars in Cell & Developmental Biology* 20:72–81.
- Møller, A. P. (1987). Variation in badge size in male House Sparrows *Passer domesticus*: Evidence for status signalling. *Animal Behaviour* 35:1637–1644.
- Møller, A. P. (1988). Badge size in the House Sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology* 22:373–378.
- Møller, A. P. (1990). Sexual behavior is related to badge size in the House Sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology* 27:23–29.
- Møller, A. P. (1992). Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238–240.
- Moreno, J., and J. J. Soler (2011). Sources of distinctness of juvenile plumage in western Palearctic passerines. *Biological Journal of the Linnean Society* 102:440–454.
- Morrison, E. S., and A. V. Badyaev (2016). Structuring evolution: Biochemical networks and metabolic diversification in birds. *BMC Evolutionary Biology* 16:168.
- Mottram, J. C. (1916). An experimental determination of the factors which cause patterns to appear conspicuous in nature. *Proceedings of the Zoological Society of London* 86:383–419.
- Mundy, N. I. (2005). A window on the genetics of evolution: *MC1R* and plumage colouration in birds. *Proceedings of the Royal Society B* 272:1633–1640.
- Mundy, N. I., N. S. Badcock, T. Hart, K. Scribner, K. Janssen, and N. J. Nadeau (2004). Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science* 303:1870–1873.
- Mundy, N. I., J. Stapley, C. Bennison, R. Tucker, H. Twyman, K. W. Kim, T. Burke, T. R. Birkhead, S. Andersson, and J. Slate (2016). Red carotenoid coloration in the Zebra Finch is controlled by a cytochrome P450 gene cluster. *Current Biology* 26:1435–1440.
- Musgrove, A. B., and K. L. Wiebe (2016). Condition-dependent expression of carotenoid- and melanin-based plumage colour of Northern Flicker nestlings revealed by manipulation of brood size. *Journal of Avian Biology* 47:176–184.
- Nachman, M. W., H. E. Hoekstra, and S. L. D'Agostino (2003). The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Sciences USA* 100:5268–5273.
- Nakagawa, S., N. Ockendon, D. O. S. Gillespie, B. J. Hatchwell, and T. Burke (2007). Assessing the function of House Sparrows' bib size using a flexible meta-analysis method. *Behavioral Ecology* 18:831–840.
- Negro, J. J., G. R. Bortolotti, and J. H. Sarasola (2007). Deceptive plumage signals in birds: Manipulation of predators or prey? *Biological Journal of the Linnean Society* 90:467–477.
- Neguer, J., and M. Manceau (2017). Embryonic patterning of the vertebrate skin. *Reviews in Cell Biology and Molecular Medicine* 3:1–29.
- Norris, K. (1993). Heritable variation in a plumage indicator of viability in male Great Tits *Parus major*. *Nature* 362:537–539.
- Norris, K. J. (1990a). Female choice and the evolution of the conspicuous plumage coloration of monogamous male Great Tits. *Behavioral Ecology and Sociobiology* 26:129–138.
- Norris, K. J. (1990b). Female choice and the quality of parental care in the Great Tit *Parus major*. *Behavioral Ecology and Sociobiology* 27:275–281.
- Oishi, I., K. Yoshii, D. Miyahara, H. Kagami, and T. Tagami (2016). Targeted mutagenesis in chicken using CRISPR/Cas9 system. *Scientific Reports* 6:23980.
- Olsen, K. (2018). *Gulls of the World: A Photographic Guide*. Princeton University Press, Princeton, NJ, USA.
- Omland, K. E. (1997). Examining two standard assumptions of ancestral reconstructions: Repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution* 51:1636–1646.
- Omland, K. E., and S. M. Lanyon (2000). Reconstructing plumage evolution in orioles (*Icterus*): Repeated convergence and reversal in patterns. *Evolution* 54:2119–2133.
- Osorio, D., and M. Vorobyev (2005). Photoreceptor spectral sensitivities in terrestrial animals: Adaptations for luminance and colour vision. *Proceedings of the Royal Society B* 272:1745–1752.
- Palleroni, A., C. T. Miller, M. Hauser, and P. Marler (2005). Predation: Prey plumage adaptation against falcon attack. *Nature* 434:973–974.
- Pardal, S., J. A. Alves, P. G. Mota, and J. A. Ramos (2018). Dressed to impress: Breeding plumage as a reliable signal of innate immunity. *Journal of Avian Biology* 49:e01579.
- Park, T. S., H. J. Lee, K. H. Kim, J. S. Kim, and J. Y. Han (2014). Targeted gene knockout in chickens mediated by TALENs. *Proceedings of the National Academy of Sciences USA* 111:12716–12721.
- Pärt, T., and A. Qvarnström (1997). Badge size in Collared Flycatchers predicts outcome of male competition over territories. *Animal Behaviour* 54:893–899.
- Pérez-Rodríguez, L., R. Jovani, and F. Mougeot (2013). Fractal geometry of a complex plumage trait reveals bird's quality. *Proceedings of the Royal Society B* 280:20122783.
- Pérez-Rodríguez, L., R. Jovani, and M. Stevens (2017). Shape matters: Animal colour patterns as signals of individual quality. *Proceedings of the Royal Society B* 284:20162446.
- Poelstra, J. W., N. Vijay, C. M. Bossu, H. Lantz, B. Ryll, I. Müller, V. Baglione, P. Unneberg, M. Wikelski, M. G. Grabherr, and J. B. Wolf (2014). The genomic landscape underlying phenotypic integrity in the face of gene flow in crows. *Science* 344:1410–1414.
- Pollard, K. A., and D. T. Blumstein (2011). Social group size predicts the evolution of individuality. *Current Biology* 21:413–417.
- Pöysä, H. (1988). Feeding consequences of the dominance status in Great Tit *Parus major* groups. *Ornis Fennica* 65:69–75.

- Price, T. (1998). Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London, Series B* 353:251–260.
- Price, T., and M. Pavelka (1996). Evolution of a colour pattern: History, development, and selection. *Journal of Evolutionary Biology* 9:451–470.
- Price-Waldman, R. M., A. J. Shultz, and K. J. Burns (2020). Speciation rates are correlated with changes in plumage color complexity in the largest family of songbirds. *Evolution* 74:1155–1169.
- Prum, R. O. (2014). Interspecific social dominance mimicry in birds. *Zoological Journal of the Linnean Society* 172:910–941.
- Prum, R. O., and A. H. Brush (2002). The evolutionary origin and diversification of feathers. *The Quarterly Review of Biology* 77:261–295.
- Prum, R. O., and L. Samuelson (2012). The hairy-downy game: A model of interspecific social dominance mimicry. *Journal of Theoretical Biology* 313:42–60.
- Prum, R. O., and S. Williamson (2002). Reaction-diffusion models of within-feather pigmentation patterning. *Proceedings of the Royal Society of London B* 269:781–792.
- Pryke, S. R., and S. Andersson (2003). Carotenoid-based epaulettes reveal male competitive ability: Experiments with resident and floater Red-shouldered Widowbirds. *Animal Behaviour* 66:217–224.
- Pryke, S. R., S. Andersson, and M. J. Lawes (2001). Sexual selection of multiple handicaps in the Red-collared Widowbird: Female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463.
- Pugesek, B. H. (1981). Increased reproductive effort with age in the California Gull (*Larus californicus*). *Science* 212:822–823.
- Pyle, P. (1997). Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Point Reyes Station, CA, USA.
- Pyle, P. (2005a). First-cycle molts in North American Falconiformes. *Journal of Raptor Research* 39:378–385.
- Pyle, P. (2005b). Remigial molt patterns in North American Falconiformes as related to age, sex, breeding status, and life-history strategies. *The Condor* 107:823–834.
- Pyle, P. (2008). Identification Guide to North American Birds, Part II: Anatidae to Alcidae. Slate Creek Press, Point Reyes Station, CA.
- Quesada, J., and J. C. Senar (2007). The role of melanin- and carotenoid-based plumage coloration in nest defence in the Great Tit. *Ethology* 113:640–647.
- Rat, M., R. E. van Dijk, R. Covas, and C. Doutrelant (2015). Dominance hierarchies and associated signalling in a cooperative passerine. *Behavioral Ecology and Sociobiology* 69:437–448.
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Reid, W. V. (1988). Age-specific patterns of reproduction in the Glaucous-winged Gull: Increased effort with age. *Ecology* 69:1454–1465.
- Remeš, V. (2011). Yolk androgens in Great Tit eggs are related to male attractiveness, breeding density and territory quality. *Behavioral Ecology and Sociobiology* 65:1257–1266.
- Ridgway, R. (1912). Color Standards and Color Nomenclature. Washington, DC, USA.
- Riegner, M. F. (2008). Parallel evolution of plumage pattern and coloration in birds: Implications for defining avian morphospace. *The Condor* 110:599–614.
- Rohwer, S. (1975). The social significance of avian winter plumage variability. *Evolution* 29:593–610.
- Rohwer, S., and E. Røskaft (1989). Results of dyeing male Yellow-headed Blackbirds solid black: Implications for the arbitrary identity badge hypothesis. *Behavioral Ecology and Sociobiology* 25:39–48.
- Rohwer, S., S. D. Fretwell, and D. M. Niles (1980). Delayed maturation in passerine plumages and the deceptive acquisition of resources. *The American Naturalist* 115:400–437.
- Rosenthal, G. G. (2007). Spatiotemporal dimensions of visual signals in animal communication. *Annual Review of Ecology, Evolution, and Systematics* 38:155–178.
- Røskaft, E., and S. Rohwer (1987). An experimental study of the function of the red epaulettes and the black body colour of male Red-winged Blackbirds. *Animal Behaviour* 35:1070–1077.
- Roulin, A. (2004). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews of the Cambridge Philosophical Society* 79:815–848.
- Saether, S. A., P. Fiske, J. A. Kålås, and J. M. Gjøl (2000). Females of the lekking Great Snipe do not prefer males with whiter tails. *Animal Behaviour* 59:273–280.
- Sætre, G.-P., T. Moum, S. Bureš, M. Král, M. Adamjan, and J. Moreno (1997). A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387:589–592.
- San-Jose, L. M., A. L. Ducrest, V. Ducret, C. Simon, H. Richter, K. Wakamatsu, and A. Roulin (2017). *MC1R* variants affect the expression of melanocortin and melanogenic genes and the association between melanocortin genes and coloration. *Molecular Ecology* 26:259–276.
- Santos, E. S. A., D. Scheck, and S. Nakagawa (2011). Dominance and plumage traits: Meta-analysis and meta-regression analysis. *Animal Behaviour* 82:3–19.
- Savalli, U. M. (1995). The evolution of bird coloration and plumage elaboration. *Current Ornithology* 12:141–190.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.
- Scott, D. K., and T. H. Clutton-Brock (1990). Mating systems, parasites and plumage dimorphism in waterfowl. *Behavioral Ecology and Sociobiology* 26:261–273.
- Scott-Samuel, N. E., R. Baddeley, C. E. Palmer, and I. C. Cuthill (2011). Dazzle camouflage affects speed perception. *PLOS One* 6:e20233.
- Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. MacGregor, D. R. Rubenstein, J. A. Uy, J. T. Weir, L. A. Whittingham, and R. J. Safran (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B* 280:20131065.
- Senar, J. (2006). Color displays as intrasexual signals of aggression and dominance. In *Bird Coloration: Function, and Evolution*, Vol. 2 (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, London, UK.
- Senar, J. C., M. J. Conroy, J. Quesada, and F. Mateos-Gonzalez (2014). Selection based on the size of the black tie of the Great Tit may be reversed in urban habitats. *Ecology and Evolution* 4:2625–2632.

- Senar, J. C., J. Domènech, and M. Camerino (2005). Female Siskins choose mates by the size of the yellow wing stripe. *Behavioral Ecology and Sociobiology* 57:465–469.
- Sepers, B., K. van den Heuvel, M. Lindner, H. Viitaniemi, A. Husby, and K. van Oers (2019). Avian ecological epigenetics: Pitfalls and promises. *Journal of Ornithology* 160:1183–1203.
- Sherley, R., T. Burghardt, P. Barham, N. Campbell, and I. Cuthill (2010). Spotting the difference: Towards fully-automated population monitoring of African Penguins *Spheniscus demersus*. *Endangered Species Research* 11:101–111.
- Shultz, A. J., and K. J. Burns (2013). Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Molecular Phylogenetics and Evolution* 66:112–125.
- Shultz, A. J., and K. J. Burns (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution* 71:1061–1074.
- Slagsvold, T., S. Dale, and A. Kruszewicz (1995). Predation favours cryptic coloration in breeding male Pied Flycatchers. *Animal Behaviour* 50:1109–1121.
- Smith, D. G. (1972). The role of the epaulets in the Red-winged Blackbird, (*Agelaius phoeniceus*) social system. *Behaviour* 41:251–268.
- Soma, M., and L. Z. Garamszegi (2018). Evolution of patterned plumage as a sexual signal in estrildid finches. *Behavioral Ecology* 29:676–685.
- Somveille, M., K. L. Marshall, and T. L. Gluckman (2016). A global analysis of bird plumage patterns reveals no association between habitat and camouflage. *PeerJ* 4:e2658.
- Steinley D. (2006). K-means clustering: A half-century synthesis. *British Journal of Mathematical and Statistical Psychology* 59:1–34.
- Stevens, M., and S. Merilaita (2009). Animal camouflage: Current issues and new perspectives. *Philosophical Transactions of the Royal Society of London, Series B* 364:423–427.
- Stevens, M., and S. Merilaita (2011). *Animal Camouflage: Mechanisms and Function*. Cambridge University Press, Cambridge, UK.
- Stevens, M., C. A. Párraga, I. C. Cuthill, J. C. Partridge, and T. S. Troscianko (2007). Using digital photography to study animal coloration. *Biological Journal of the Linnean Society* 90:211–237.
- Stevens, M., J. Troscianko, J. K. Wilson-Aggarwal, and C. N. Spottiswoode (2017). Improvement of individual camouflage through background choice in ground-nesting birds. *Nature Ecology & Evolution* 1:1325–1333.
- Stevens, M., D. H. Yule, and G. D. Ruxton (2008). Dazzle coloration and prey movement. *Proceedings of the Royal Society B* 275:2639–2643.
- Stoddard, M. C., and D. Osorio (2019). Animal coloration patterns: Linking spatial vision to quantitative analysis. *The American Naturalist* 193:164–186.
- Stoddard, M. C., and R. O. Prum (2008). Evolution of avian plumage color in a tetrahedral color space: A phylogenetic analysis of New World buntings. *The American Naturalist* 171:755–776.
- Stoddard, M. C., and R. O. Prum (2011). How colorful are birds? Evolution of the avian plumage color gamut. *Behavioral Ecology* 22:1042–1052.
- Stoddard, M. C., and M. Stevens. (2010). Pattern mimicry of host eggs by the Common Cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B* 277:1387–1393.
- Stoddard, M. C., R. M. Kilner, and C. Town (2014). Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nature Communications* 5:4117.
- Stoddard, M. C., K. Kupán, H. N. Eyster, W. Rojas-Abreu, M. Cruz-López, M. A. Serrano-Meneses, and C. Küpper (2016). Camouflage and clutch survival in plovers and terns. *Scientific Reports* 6:32059.
- Stryjewski, K. F., and M. D. Sorenson (2017). Mosaic genome evolution in a recent and rapid avian radiation. *Nature Ecology & Evolution* 1:1912–1922.
- Swaddle, J. P., and I. C. Cuthill (1994). Female Zebra Finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society B* 258:267–271.
- Swaddle, J. P., and M. Witter (1994). Food, feathers and fluctuating asymmetries. *Proceedings of the Royal Society B* 255:147–152.
- Takahashi, M., H. Arita, M. Hiraiwa-Hasegawa, and T. Hasegawa (2008). Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour* 75:1209–1219.
- Tankus, A., and Y. Yeshurun (2009). Computer vision, camouflage breaking and countershading. *Philosophical Transactions of the Royal Society of London, Series B* 364:529–536.
- Tarof, S. A., P. O. Dunn, and L. A. Whittingham (2005). Dual functions of a melanin-based ornament in the Common Yellowthroat. *Proceedings of the Royal Society B* 272:1121–1127.
- Taylor, S., and L. Campagna (2016). Evolution. Avian supergenes. *Science* 351:446–447.
- Thayer, A. H. (1896). The law which underlies protective coloration. *The Auk* 13:124–129.
- Thayer, G. (1909). *Concealing-coloration in the animal kingdom: An exposition of the laws of disguise through color and pattern: Being a summary of Abbott H. Thayer's discoveries*. Macmillan, New York, NY, USA.
- Theron, E., K. Hawkins, E. Bermingham, R. E. Ricklefs, and N. I. Mundy (2001). The molecular basis of an avian plumage polymorphism in the wild: A melanocortin-1-receptor point mutation is perfectly associated with the melanin plumage morph of the Bananaquit. *Proceedings of the Royal Society B* 11:550–557.
- Thusius, K. J. (2001). Extrapair paternity is influenced by breeding synchrony and density in the Common Yellowthroat. *Behavioral Ecology* 12:633–639.
- Tibbetts, E. A. (2008). Resource value and the context dependence of receiver behaviour. *Proceedings of the Royal Society B* 275:2201–2206.
- Tibbetts, E. A., and J. Dale (2007). Individual recognition: It is good to be different. *Trends in Ecology & Evolution* 22:529–537.
- Toews, D. P. L., L. Campagna, S. A. Taylor, C. N. Balakrishnan, D. T. Baldassarre, P. E. Deane-Coe, M. G. Harvey, D. M. Hooper, D. E. Irwin, C. D. Judy, et al. (2016a). Genomic approaches to understanding population divergence and speciation in birds. *The Auk: Ornithological Advances* 133:13–30.
- Toews, D. P. L., N. R. Hofmeister, and S. A. Taylor (2017). The evolution and genetics of carotenoid processing in animals. *Trends in Genetics* 33:171–182.
- Toews, D. P., S. A. Taylor, R. Vallender, A. Brelsford, B. G. Butcher, P. W. Messer, and I. J. Lovette (2016b). Plumage genes and little

- else distinguish the genomes of hybridizing warblers. *Current Biology* 26:2313–2318.
- Toomey, M. B., C. I. Marques, P. Andrade, P. M. Araújo, S. Sabatino, M. A. Gazda, S. Afonso, R. J. Lopes, J. C. Corbo, and M. Carneiro (2018). A non-coding region near *Follistatin* controls head colour polymorphism in the Gouldian Finch. *Proceedings of the Royal Society B* 285:20181788.
- Troscianko, J., and M. Stevens (2015). Image calibration and analysis toolbox – A free software suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and Evolution* 6:1320–1331.
- Troscianko, J., J. Wilson-Aggarwal, C. N. Spottiswoode, and M. Stevens (2016a). Nest covering in plovers: How modifying the visual environment influences egg camouflage. *Ecology and Evolution* 6:7536–7545.
- Troscianko, J., J. Wilson-Aggarwal, M. Stevens, and C. N. Spottiswoode (2016b). Camouflage predicts survival in ground-nesting birds. *Scientific Reports* 6:19966.
- Turing, A. (1952). The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society B* 237:37–72.
- Tuttle, E. M., A. O. Bergland, M. L. Korody, M. S. Brewer, D. J. Newhouse, P. Minx, M. Stager, A. Betuel, Z. A. Cheviron, W. C. Warren, R. A. Gonser, and C. N. Balakrishnan (2016). Divergence and functional degradation of a sex chromosome-like supergene. *Current Biology* 26:344–350.
- Uy, J. A., R. G. Moyle, and C. E. Filardi (2009a). Plumage and song differences mediate species recognition between incipient flycatcher species of the Solomon Islands. *Evolution* 63:153–164.
- Uy, J. A., R. G. Moyle, C. E. Filardi, and Z. A. Cheviron (2009b). Difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor. *The American Naturalist* 174:244–254.
- Van Belleghem, S. M., R. Papa, H. Ortiz-Zuazaga, F. Hendrickx, C. D. Jiggins, W. O. McMillan, and B. A. Counterman (2018). patternize: An R package for quantifying colour pattern variation. *Methods in Ecology and Evolution* 9: 390–398.
- Veiga, J. P. (1993). Badge size, phenotypic quality, and reproductive success in the House Sparrow: A study on honest advertisement. *Evolution* 47:1161–1170.
- Véron, N., Z. Qu, P. A. Kipen, C. E. Hirst, and C. Marcelle (2015). CRISPR mediated somatic cell genome engineering in the chicken. *Developmental Biology* 407:68–74.
- Vignieri, S. N., J. G. Larson, and H. E. Hoekstra (2010). The selective advantage of crypsis in mice. *Evolution* 64:2153–2158.
- Vinther, J. (2015). A guide to the field of palaeo colour: Melanin and other pigments can fossilise: Reconstructing colour patterns from ancient organisms can give new insights to ecology and behaviour. *BioEssays* 37:643–656.
- von Helversen, B., L. J. Schooler, and U. Czienskowski (2013). Are stripes beneficial? Dazzle camouflage influences perceived speed and hit rates. *PLOS One* 8:e61173.
- Vorobyev, M., and D. Osorio (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B* 265:351–358.
- Vorobyev, M., R. Brandt, D. Peitsch, S. B. Laughlin, and R. Menzel (2001). Colour thresholds and receptor noise: Behaviour and physiology compared. *Vision Research* 41:639–653.
- Vorobyev, M., D. Osorio, A. T. Bennett, N. J. Marshall, and I. C. Cuthill (1998). Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* 183:621–633.
- Wallace, A. (1877). The colors of animals and plants. *The American Naturalist* 11:641–662.
- Watterson, R. L. (1942). The morphogenesis of down feathers with special reference to the developmental history of melanophores. *Physiological Zoology* 15:234–259.
- Weaver, R. J., R. E. Koch, and G. E. Hill (2017). What maintains signal honesty in animal colour displays used in mate choice? *Philosophical Transactions of the Royal Society B* 372:20160343.
- Weibel, A. C., and W. S. Moore (2005). Plumage convergence in *Picoides* woodpeckers based on a molecular phylogeny, with emphasis on convergence in Downy and Hairy woodpeckers. *The Condor* 107:797–809.
- Weinstein, B. G. (2018). A computer vision for animal ecology. *The Journal of Animal Ecology* 87:533–545.
- Wellenreuther, M., and L. Bernatchez (2018). Eco-evolutionary genomics of chromosomal inversions. *Trends in Ecology & Evolution* 33:427–440.
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* 58:155–183.
- Westneat, D. F. (2006). No evidence of current sexual selection on sexually dimorphic traits in a bird with high variance in mating success. *The American Naturalist* 167:e171–e189.
- Whitekiller, R. R., D. F. Westneat, P. L. Schwagmeyer, and D. W. Mock (2010). Badge size and extra-pair fertilizations in the House Sparrow. *The Condor* 64:1461–1471.
- Whitfield, D. P. (1986). Plumage variability and territoriality in breeding turnstone *Arenaria interpres*: Status signalling or individual recognition? *Animal Behaviour* 34:1471–1482.
- Whitfield, D. P. (1987). Plumage variability, status signalling and individual recognition in avian flocks. *Trends in Ecology & Evolution* 2:13–18.
- Wilson-Aggarwal, J. K., J. T. Troscianko, M. Stevens, and C. N. Spottiswoode (2016). Escape distance in ground-nesting birds differs with individual level of camouflage. *The American Naturalist* 188:231–239.
- Witzel, C., and K. R. Gegenfurtner (2018). Color perception: Objects, constancy, and categories. *Annual Review of Vision Science* 4:475–499.
- Woodcock, M. E., A. Idoko-Akoh, and M. J. McGrew (2017). Gene editing in birds takes flight. *Mammalian Genome* 28:315–323.
- Young, C. M., K. E. Cain, N. Svedin, P. R. Y. Backwell, and S. R. Pryke (2016). The role of pigment based plumage traits in resolving conflicts. *Journal of Avian Biology* 47:167–175.
- Yu, M., Z. Yue, P. Wu, D.-Y. Wu, J.-A. Mayer, M. Medina, R. B. Wideltz, T.-X. Jiang, and C.-M. Chuong (2004). The developmental biology of feather follicles. *International Journal of Developmental Biology* 48:181–191.
- Zink, B., and J. Remsen (1986). Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology* 4:1–69.