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REVIEW

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ABSTRACT
Avian plumage has captivated scientists and the public alike for generations and has been a fundamental study system for research into signal evolution. By contrast, relatively little attention has been paid to avian bare parts such as exposed skin, bills, feet, and combs, despite considerable variation in structure and coloration within and between species. To better understand the potential signaling role of bare parts, we conducted a comprehensive literature search that returned 321 published studies. In reviewing these studies, we found that (1) bare-part color is widely distributed taxonomically and is produced by diverse mechanisms; (2) many bare parts are likely to be dynamic, honest signals of current condition or status and can also reflect genetic makeup and early developmental conditions; and (3) bare parts can function as pluripotent social signals, mediating interactions between competitors, mates, and kin. Differences between bare parts and plumage in phenology and information content support a multiple-messages interpretation of their respective signaling roles, in that bare parts may contain information that is complementary to, but distinctive from, information conveyed by plumage-based signals. We consider it likely that a great deal of bare-part variation is "hidden in plain sight," in that meaningful variation may not be recorded by many current studies. We urge more careful and extensive characterization of bare-part coloration in a wider range of species because of its potential to advance our understanding of signal function and constraints, with particular reference to the role of dynamic color signals and the evolution of multiple ornamentation.

Keywords: bare parts, carotenoids, color, honest signal, melanin, multiple ornamentation, phenology, plumage, soft parts

El rol de señalización de las partes desnudas en las aves

RESUMEN
El plumaje de las aves ha cautivado por generaciones a científicos y público en general por igual, y ha sido un sistema de estudio fundamental para la investigación de la evolución de las señales. En contraste, se ha prestado relativamente poca atención a las partes desnudas de las aves cómo piel expuesta, picos, patas y crestas, a pesar de la variación considerable que existe en estructura y coloración dentro y entre especies. Para entender mejor el rol potencial de señalización de las partes desnudas, realizamos una revisión bibliográfica exhaustiva, que dio como resultado 321 estudios publicados y apoyó las siguientes conclusiones: (1) el color de la parte desnuda está ampliamente distribuido en términos taxonómicos y es producido por diversos mecanismos; (2) muchas partes desnudas son probablemente señales honestas dinámicas de la condición o del estatus actual y pueden reflejar también la composición genética y las condiciones tempranas de desarrollo; (3) las partes desnudas pueden funcionar como señales sociales pluripotenciales, mediando interacciones entre competidores, compañeros y parientes. Las diferencias en fenología y en contenido de información entre las partes desnudas y el plumaje apoyan la interpretación de que cumplen distintos roles de señalización mediante la transmisión de múltiples mensajes, en el sentido de que las partes desnudas podrían contener información que es complementaria pero distinta de la información transmitida por las señales basadas en el plumaje. Consideramos probable que exista una gran cantidad de variación en las partes desnudas que esté "oculta a simple vista", en el sentido de que una gran cantidad de variación puede no estar registrada en muchos estudios actuales. Instamos a una caracterización más cuidadosa y extensa de la coloración de las partes desnudas en un rango más amplio de especies, debido al potencial que presenta para promover el conocimiento sobre la función y las restricciones de la señalización, en particular con respecto al rol de las señales de color dinámicas y la evolución de ornamentaciones múltiples.

Palabras clave: carotenoides, color, fenología, melanina, partes blandas, partes desnudas, ornamentación múltiple, plumaje, señales honestas

INTRODUCTION

Visual signals are used by animals to mediate intraspecific interactions related to social selection (*sensu* Lyon and Montgomerie 2012), including mate choice (Parker and Ligon 2003, Locatello et al. 2012), competition over resources (Hamilton et al. 2013, Dwyer 2014), and parent–offspring communication (Saino et al. 2003, Morales et al. 2009a). The brightly colored plumage of many bird species provides a popular system for the study of signal evolution and has played a crucial role in demonstrating the importance of honest signals in dominance and mate-choice interactions (Hill and McGraw 2006a, 2006b). Less well appreciated, however, is the fact that birds have another, equally ubiquitous system of visual ornamentation: bare parts (Figure 1).

In their structure and apparent function, bare parts resemble the colorful integuments displayed by numerous taxa, including fishes, reptiles, and primates. In fishes, integumentary coloration can reflect status, nutrition, and parasitism and is evaluated by competitors and mates (Kodric-Brown 1985, 1998, Dijkstra et al. 2007, Locatello et al. 2012, Sefc et al. 2014). Reptiles use dermal pigments for signaling as well (Macedonia et al. 2000, Hamilton et al. 2013, Polo-Cavia et al. 2013, Ibáñez et al. 2014), whereas primates use colorful bare skin to signal dominance and sexual receptivity (Setchell 2005, Changizi et al. 2006, Setchell et al. 2008, Dubuc et al. 2009). Although there has been active research on bare-part color in birds, our understanding of the functionality of these traits remains limited, in comparison both to bare parts in other taxa (e.g., fishes) and to plumage-based traits in birds. For instance, an influential review of carotenoid coloration in birds identified only 14 studies of bare parts, compared to 130 studies of plumage (McGraw 2006), despite the fact that carotenoids are thought to be more common in bare parts than in plumage (Olson and Owens 2005). Another review listed 18 studies of mate choice in relation to bare parts and 107 in relation to plumage (Hill 2006). Moreover, although there have been several important reviews on aspects of plumage coloration in recent years (Roulin 2004, Hawkins et al. 2012, Parker 2013, LaFountain et al. 2015), we are not aware of any holistic review of bare-part coloration and signaling (but see Negro et al. 2006).

Although bare parts and plumage are often colored by the same pigments (Hill and McGraw 2006a, 2006b), there are differences between them that may have important implications for signal function and evolution. Like the integumentary colors of many species of fishes, reptiles, and primates, bare-part color is flexible. Whereas feather coloration is relatively static within a season because of constraints imposed by molt schedules, bare-part coloration has the potential to change color within weeks, days, hours, or even seconds (Gautier et al. 2008, Morales et al.
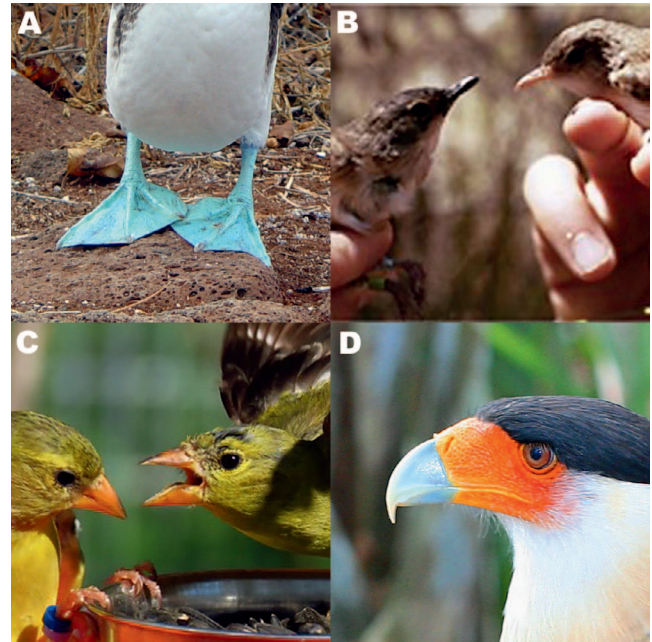
FIGURE 1. Bare-part color is widely distributed taxonomically among birds and is produced by diverse mechanisms, including carotenoids, melanin, structural coloration, and hemoglobin. (**A**–**D**) Examples of species whose bare-part colors illustrate major findings of this review. (**A**) Legs and feet of a male Blue-footed Booby (*Sula nebouxii*). The blue coloration is structural, whereas carotenoids give the feet a greenish hue, which serves as an honest signal of quality in mate-choice interactions and reproductive-investment decisions between partners. (**B**) Bill coloration of 2 male Red-backed Fairywrens (*Malurus melanocephalus*), a melanin-based trait that changes from beige (nonbreeding, right) to black (breeding, left) in response to changes in social status. (**C**) Bill coloration of 2 female American Goldfinches (*Spinus tristis*), a carotenoid-based trait used as an intrasexual signal of dominance among females but not males. (**D**) The cere of a male Crested Caracara (*Caracara cheriway*), which is colored primarily by hemoglobin. During agonistic interactions, the cere of the aggressing bird turns pale within seconds. See text for more details on these and other examples of signaling with bare parts. Photo credits: Blue-footed Booby and Crested Caracara from Wikimedia Commons; Red-backed Fairywrens courtesy of J. Karubian; American Goldfinches courtesy of K. Tarvin

2009b, Rosenthal et al. 2012, Dwyer 2014). Receivers respond to this short-term variation in contexts including mate choice, agonistic interactions, and parental care (Velando et al. 2006, Dugas 2009, Simons and Verhulst 2011, Dwyer 2014). Bare-part and plumage coloration may also be constrained by different physiological trade-offs: among species with both types of ornaments of a similar coloration, variation in bare-part color can be uncorrelated with variation in plumage color, indicating that the 2 ornaments may reflect different aspects of condition (Jawor and Breitwisch 2004, Rosen and Tarvin 2006, Laucht and Dale 2012). These facts suggest that the

signaling role of bare parts may be distinct from that of plumage, but this possibility remains poorly explored. For these reasons, a better knowledge of bare-part signals and their interplay with plumage is likely to improve our understanding of signal evolution in birds, including the causes and consequences of multiple ornamentation (Møller and Pomiankowski 1993, Candolin 2003) and female ornamentation (Amundsen 2000), as well as the role of social selection in driving phenotypic variation (Lyon and Montgomerie 2012).

We conducted a comprehensive literature search with the goal of understanding the nature of the information conveyed by bare parts, the social contexts in which bare parts may be employed as signals, and how and why these may differ from plumage-based signals. In reviewing the available literature on bare-part coloration, we documented correlations between color and socio-ecological variables both within and across species, responses of bare-part color to experimental manipulations, and responses of receivers to color manipulations. Here, we present a synthetic review of bare-part coloration in birds in the context of current signaling theories, concluding that avian bare parts are likely to be flexible, condition-dependent social signals that mediate communication between competitors, kin, and potential mates. We argue that the importance of bare-part coloration has been underappreciated in many avian systems, and we highlight priority themes for future research.

SCOPE OF THIS REVIEW

To find studies of bare parts, we searched Web of Science for articles (dating from 1976, where Web of Science begins, to the present) containing combinations of the terms *color, signal, bird, bare part, soft part, bill, legs, feet, comb, wattle, caruncle, eye-ring, eye, cere, lore, gape, carotenoid, melanin, structural color, parasite, diet, testosterone, mate choice, competition,* and *color change.* We then completed a secondary search using names of any bird species that were identified in studies found in the primary search. Finally, we followed references from studies returned by the primary and secondary searches to identify other studies with potentially relevant results, including those published before 1976. We read all studies and recorded all reported correlative or experimental tests of a relationship between the color or size properties of a bare part and any social, physiological, or ecological variable. Our search returned a total of 321 peer-reviewed publications on 101 species in 38 families (Supplemental Material Appendix A).

We include under the term *bare parts* a variety of integumentary structures in birds that are not covered by feathers, including the bill, legs, and feet, regions of exposed bare skin on the head and neck, and unfeathered lores, eye-rings, pouches, and sacs. In addition to patches of bare skin, some birds display fleshy outgrowths of the cere or combs, wattles, snoods, tubercles, and caruncles on the face. We also include the gape, or interior of the mouth, and the iris, which are conspicuously colored in some birds. In addition to color, we also gathered information on the size of these fleshy bare parts, which covaries with many of the same properties as color and may be evaluated similarly to variation in patch size in plumage signals.

Although we have comprehensive visual descriptions of all known birds (del Hoyo et al. 2011), plates fail to capture the range and subtleties of color variation in the bare parts of wild birds. For instance, there may be subtle variation in coloration within the same individual over time or between sexes and age classes that is detectable only with a spectrophotometer or through digital imaging (e.g., Villafuerte and Negro 1998). In addition, the same trait value, such as black bill coloration, may serve as a signal in some species (e.g., House Sparrows [*Passer domesticus*], in which the bills of adult males become black for the breeding season; Laucht and Dale 2012) but not in others (e.g., ravens [*Corvus* spp.], in which all birds have black bills, including nestlings; del Hoyo et al. 2011). At present, we lack the basic knowledge needed to determine the degree to which, and the context in which, bare parts serve as signals for most species. There are several reasons why this information is currently lacking, including the logistical difficulties of field-based measures of bare-part coloration vs. feathers (feathers can be nonlethally collected from free-living birds and measured in the laboratory with a photospectrometer, and bare-part coloration has been noted to fade over time in museum specimens; Kennedy 2010) and of obtaining measures at multiple time points. For this reason, the data generated by descriptive studies of bare-part color variation in living birds are crucial to our ability to ask broader questions about the ecology and evolution of this phenomenon.

We also point out that a color–condition relationship in a given trait does not necessarily mean that the trait in question operates as a signal; evidence of a receiver response to natural or experimentally induced variation in ornament value is needed to reach that conclusion. Throughout this article, we employ the definition of *signal* given by Scott-Phillips (2008): an act or structure that induces a response from a receiver and that is adaptive for both the signaler and the receiver. However, because selection upon signals is rarely quantified in the literature, we have adopted a heuristic definition, using the term *signal* when an act or structure can be shown to reflect information about its bearer and to cause an appropriate response given the information that is being conveyed. When an act or structure reflects information but no receiver response has been investigated, we refer to it as a

"putative" or "potential" signal. We refer to acts or structures that are adaptive for receivers to observe but not for signalers to send as *cues* (*sensu* Scott-Phillips 2008). An *ornament* is a structure that is the target of mate choice (*sensu* McCullough et al. 2016).

It is worth noting that the studies conducted on bare-part coloration to date are not evenly distributed across the entire avian phylogeny. Instead, as is often the case, species are selected for a particular line of research because they are logistically feasible to work with or because there is an a priori likelihood that a certain relationship may be found. In practice, this means that many of the species included in our review are found in North America or Europe and present bright, carotenoid-colored bare parts. The dataset is also heavily biased toward common and well-studied species used in genetic and immunological research (i.e. Zebra Finch [*Taeniopygia guttata*] and Common Blackbird [*Turdus merula*]) and those in which sexual selection has been the focus (i.e. Phasianidae). A variety of strange and brightly colored bare parts can be observed in tropical species such as wattle-eyes (Platysteiridae) and honey-eaters (Meliphagidae) that are rarely studied and nearly absent from our dataset.

The same bias may also extend to mechanisms of coloration. For example, although carotenoid-based coloration is well studied in birds, we know little about the constraints on melanin and structural colors and even less about behavioral color changes such as hemoglobin flushing and turgor-pressure changes. Accessory pigments like pterins and psittacofulvins are as yet unknown from bare parts, but there may be more pigments coloring bare parts than are currently recognized. As such, a more nuanced understanding of the mechanisms by which pigments are deposited, metabolized, displayed, and removed, as well as their fate after removal, will help us understand the information conveyed by color in bare parts.

DISTRIBUTION AND DIVERSITY OF BARE PARTS

Our search returned studies of bare-part coloration in 38 families (Table 1), largely in the orders Galliformes, Anseriformes, Charadriiformes, Falconiformes, and Passeriformes. Bare parts are typically vascularized epidermal tissue (Stettenheim 2000) that is colored by transport and deposition of pigments through the blood stream (carotenoids), by pigment production in situ by specialized cells (melanin), by hemoglobin under the skin (i.e. flushing), or by structural coloration in the dermis. Interested readers can find large and nearly comprehensive datasets on the occurrence of carotenoid color (Olson and Owens 2005, Dey et al. 2015), structural color (Prum and Torres 2003), and hemoglobin flushing (Negro et al. 2006) in bare parts.

Carotenoid-colored Bare Parts

Carotenoids were the most common source of bare-part coloration in our dataset (studied in 60 species in 29 families; Table 1). Carotenoids are large, lipid-soluble molecules that are responsible for much of the yellow, orange, and red coloration in animals (Goodwin 1984), and these pigments have been studied extensively as colorants of bird feathers (McGraw 2006). Birds must obtain carotenoids exogenously through their diet, but after consumption some carotenoids may be metabolized into novel forms (Ligon et al. 2016). Because carotenoids are involved in many physiological pathways and trade-offs (Svensson and Wong 2011), variation in plasma carotenoid levels (Bortolotti et al. 1996, McGraw et al. 2003), along with the metabolism of carotenoid pigments at the integument (McGraw 2004, Pérez-Rodríguez et al. 2016), leads to intraspecific variation in bare-part coloration that is often interpreted as an honest signal of quality or condition.

Carotenoid-based coloration is thought to be more common and widespread in bare parts than in plumage (Olson and Owens 2005). One study estimated that 8% of passerines have carotenoid-colored bills (Dey et al. 2015), and colorful bare parts that are likely produced by carotenoids are present in all major avian lineages, from the paleognaths to the passerines (del Hoyo et al. 2011). The mechanisms for displaying carotenoids in vascular tissue are present in fish (Endler 1980, 1983, Sefc et al. 2014), amphibians (Brenes-Soto and Dierenfeld 2014), and reptiles (Fitze et al. 2009, Ibáñez et al. 2014) and may predate their display in feathers. Although some researchers have argued for multiple independent evolutionary origins of carotenoid-based plumage (Stoddard and Prum 2011, Thomas et al. 2014), the distribution of colorful bare parts among contemporary avian families suggests that this trait is likely to be ancestral in birds. The display of red carotenoids is possible only through the metabolism of yellow carotenoids in the skin (McGraw 2004) and liver (del Val et al. 2009). Recent studies indicate that the display of red carotenoids in bare parts is contingent on the presence of functioning copies of the ketolase genes known as CYP2J19 (Mundy et al. 2016), whereas their display in plumage requires these genes as well as additional genes related to integumentary development that may bind pigments to the growing feather (Ligon et al. 2016, Lopes et al. 2016). The need for additional epidermal differentiation genes in order to achieve carotenoid-colored plumage might partially explain why carotenoid coloration is more commonly observed in bare parts. Carotenoids in bare skin, unlike in feathers, are protected from photodegradation by esterification (McGraw 2004, Walsh et al. 2012, Pérez-Rodríguez et al. 2016), which suggests they might be withdrawn for use at a later date; however, experimental evidence suggests that colorful skin

TABLE 1. Bird families in which bare-part coloration has been investigated in the context of signaling, with number of species investigated, number of published studies, and reported bare-part types (C = carotenoids; M = melanin; S = structural; H = hemoglobin; F = fleshy ornament, the size of which often covaries with many of the same properties as color; UV = ultraviolet component of the color signal).

Family	Species (n)	Studies (n)	Bare-part type	Example
Anatidae	6	10	C, S, F	Omland 1996a, 1996b
Cracidae	2	1	F	Buchholz 1991
Phasianidae	14	75	C, S, H, UV, F	Pérez-Rodríguez and Viñuela 2008
Spheniscidae	3	12	C, UV	Massaro et al. 2003
Procellariidae	1	1	C	Birkeland 2003
Ciconiidae	1	1	C	Negro et al. 2000
Threskiornithidae	1	1	C	Heath and Frederick 2006
Fregatidae	2	6	C, H	Madsen et al. 2007b
Sulidae	2	14	C, S	Velando et al. 2006
Phalacrocoracidae	1	1	C	Childress and Bennun 2002
Accipitridae	6	7	C, H, UV	Sternalski et al. 2010
Rallidae	6	15	C, F	Dey et al. 2014
Jacanidae	1	1	C, F	Emlen and Wrege 2004
Scolopacidae	1	2	F	Lozano and Lank 2004
Laridae	11	21	C, M	Møller et al. 2007
Alcidae	3	3	C	Jones and Montgomerie 1992
Columbidae	1	2	C, F	Casagrande et al. 2011
Strigidae	2	3	C, UV	Parejo et al. 2010
Apodidae	1	1	UV	Bize et al. 2006
Bucerotidae	2	1	F	Curio 2004
Falconidae	4	14	C, H	Vergara et al. 2011
Psittaculidae	1	3	S	Lahaye et al. 2014
Tyrannidae	1	1	C	Cardoni et al. 2017
Maluridae	1	3	M	Karubian et al. 2011
Meliphagidae	1	1	M	Buttemer and Astheimer 2000
Notiomystidae	1	2	C	Ewen et al. 2008
Corvidae	2	2	M	Heinrich and Marzluff 1992
Paridae	1	3	C, H	Jourdie et al. 2004
Panuridae	1	1	C	Surmacki et al. 2015
Hirundinidae	1	5	C, UV	Saino et al. 2003
Sturnidae	2	10	C, M, UV	Préault et al. 2005
Turdidae	2	14	C, UV	Baeta et al. 2008
Passeridae	2	12	C, M	Dugas and McGraw 2011
Ploceidae	2	3	C, M	Shawcross and Slater 1984
Estrildidae	5	52	C, UV	Gautier et al. 2008
Fringillidae	3	14	C, M, H	Rosenthal et al. 2012
Emberizidae	2	2	M	Clotfelter et al. 2003
Cardinalidae	2	5	C, M	Jawor et al. 2003, 2004

continuously demands new pigments (Alonso-Alvarez et al. 2004), perhaps enhancing the trade-offs associated with carotenoid signaling.

Melanin and Structural Colors

Melanin is common throughout almost all groups of animals and has recently been detected in the bare skin of an ornithischian dinosaur (Vinthner et al. 2016), which suggests that it is ancestral in avian bare parts. However, although melanin appears to be more common than carotenoids in the bare parts of birds (del Hoyo et al. 2011), it is less often studied in a signaling context (15 species, 10 families; Table 1). Melanin is synthesized endogenously by melanocytes in the epidermis, and the

physiological costs of this mode of signal production in birds—and, hence, the honesty of the signaling—are currently unclear (Jawor and Breitwisch 2003, Griffith et al. 2006, McGraw 2008). Melaninic coloration can be naturally selected for several different uses (described below), providing a potential non-signaling explanation for its commonness.

Structural coloration, which is composed of layers of dermal collagen that create color by scattering light, occurs in the skin, rhamphotheca, or podotheca of 129 families and ≥2.5% of all bird species (Prum and Torres 2003). We found studies of structural coloration in a signaling context from 8 species in 4 families (Table 1). Structural colors are often associated with the eye-ring and fleshy

facial ornaments but can also be found in bills, legs, and feet. Structural colors can appear as blues and greens or even as yellows and are typically underlain by a layer of melanosomes in the dermis, which prevents incoherent scattering by the tissues below. The importance of this melanic layer may indicate that structural colors are more likely to evolve where bare skin is already pigmented by melanin (Prum and Torres 2003). Structural collagen can also be interspersed with vacuoles of carotenoids, giving skin the combined colors of pigments and structural components (Prum and Torres 2003). Both carotenoids and structural colors can produce ultraviolet (UV) reflectance, which birds can see (Mougeot and Arroyo 2006, Mougeot et al. 2007a). UV reflectance from carotenoid-colored ornaments may be negatively correlated with carotenoid concentration (e.g., Dugas and McGraw 2011), which is likely the result of carotenoids in the epidermis obscuring the structural coloration of the dermis below (Mougeot et al. 2007a). Structural colors can change surprisingly rapidly; completely new structural coloration can develop within 2 wk in response to hormones (Nespor et al. 1996) and can possibly reflect changes in condition within 6 days (Schull et al. 2016). Many tropical birds exhibit structural bare-part coloration, which may be favored for signal transmission by the light environment of dark tropical forests (Prum and Torres 2003).

Hemoglobin and Other Rapid Changes

Two additional mechanisms of color acquistion and change have been reported for bare parts but not for plumage. Hemoglobin can be flushed into or out of bare skin to display or conceal red and purple colors, which occurs in the gapes of some nestlings and in the skin of adult birds of at least 28 genera in 20 families (Negro et al. 2006). Most are large, darkly colored birds with extensive bare skin patches on the head and neck, which may be related to thermoregulation (Negro et al. 2006; see below). Hemoglobin flushing in a signaling context was investigated in juveniles of 2 species in 2 families and in adults of 5 species in 4 families. Additionally, 2 species, the Tarictic Hornbill (*Penelopides panini*) and the Wild Turkey (*Meleagris gallopavo*), are reported to display rapid color change (on the order of seconds) in blue and white skin, possibly due to changes in turgor pressure altering structural colors (Buchholz 1995, Curio 2004). Flushing and (potentially) turgor pressure represent phenologically distinct forms of color change from the gradual accumulation of pigments or the growth of structural colors. These colors change rapidly, within seconds or minutes, in response to behavioral stimuli such as the appearance of a competitor, mate, or parent. Phenologically, these color changes resemble how some phasianids selectively erect their combs or wattles in certain situations, turning the

signal on or off at will (Mateos and Carranza 1997, Kimball and Braun 2008).

FLEXIBILITY AND CONDITION DEPENDENCE IN BARE PARTS

Many birds modify the pigmentation or structure of the integument itself over periods ranging from hours to weeks. Color–condition relationships are easily detected in carotenoid ornaments, but there are likely to be aspects of condition reflected by melanin and structural coloration as well. Because birds vary widely in the specific colors they display and the range of variability observed, studies differ in the color properties and color systems used to quantify trait expression. For instance, differences in hue, brightness, and chroma can all be indicative of changes in the quantity and quality of carotenoid pigments (Butler et al. 2011); as such, we deferred to the authors about the color metrics that can quantify trait expression in their study species. Structures that are not under social or sexual selection are not expected to display condition dependence (Andersson 1994), and for species with multiple colorful bare parts, only one might be a signal under selection. For instance, in some species, bill color conveys an aspect of condition that feet or legs with the same pigments do not (Jouventin et al. 2007, Butler and McGraw 2011, Laucht and Dale 2012).

Experimental studies using photospectrometers often detect bare-part color change at the first post-treatment measurement, typically days or weeks after treatment, which means that color could have changed appreciably earlier. For instance, the bill color of American Goldfinches (*Spinus tristis*) had dulled significantly, probably because of stress, by the first postcapture measurement only 6.5 hr later (Rosenthal et al. 2012). As such, an essential ingredient for understanding the phenology of bare-part signals is to sample color at a finer scale, in order to find the first time that color differences detectable by the avian visual system are present. For carotenoid-colored bare parts, that scale could be as fine as hourly, but even structural colors might change within days (Schull et al. 2016).

Environmental Influences

Variation in food quantity or quality, dietary carotenoids, dietary cholesterol (the carrier of carotenoids in the blood stream), and hydration can all cause changes in carotenoid bare-part coloration (McGraw and Parker 2006, Velando et al. 2006, Pérez-Rodríguez and Viñuela 2008, Morales et al. 2009b, López et al. 2011). Body size and body condition are commonly correlated with carotenoid bare-part color (Bright et al. 2004, Rosen and Tarvin 2006, Biard et al. 2010, Doutrelant et al. 2013), and in our dataset, 70% of species tested showed evidence for a positive correlation

between bare-part color or size and body condition ($n = 27$). In Blue-footed Boobies (*Sula nebouxii*), for example, food deprivation dulls carotenoid-based foot color within 48 hr, whereas supplementation restores color within 24 hr (Velando et al. 2006). In seabirds, environmental variability (such as that caused by the El Niño–Southern Oscillation) strongly affects food availability and is reflected in both melanin and carotenoid bare parts (Møller et al. 2007, Dentressangle et al. 2008, Keddar et al. 2015). Differences in resources between territories can also contribute to variation in bare-part color across the landscape (Casagrande et al. 2006). Experimental exposure to gut parasites, which inhibit carotenoid absorption and lipoprotein production (Allen 1987), can cause a decrease in comb size within 10 days in Red Grouse (*Lagopus lagopus scotica*; Mougeot et al. 2009) and a loss of carotenoid color within 2 wk in Domestic Chickens (*Gallus gallus domesticus*; Marusich et al. 1972, Baeta et al. 2008). Antiparasitic drugs can elevate color within 2 mo in American Goldfinches (Hill et al. 2009). Antiparasitics might also increase the UV signal of structural bare-part colors in King Penguins (*Aptenodytes patagonicus*) within 6 days (Schull et al. 2016). In Red Grouse, interannual and interpopulation variability in both comb size and the comb size–body condition relationship are explained by population density, local parasite burden, and climatic variability (Piertney et al. 2008, Vergara et al. 2011, 2012a, 2012b, 2012c). Environmental heterogeneity thus helps explain conflicting results regarding the condition dependence of bare parts (Vergara et al. 2012a, 2012b).

Environmental toxins can disrupt carotenoid bare-part coloration within 1 mo (Bortolotti et al. 2003, Pérez et al. 2010a, 2010b), and challenges to both the innate and acquired immune system typically result in duller carotenoid bare parts within days or weeks (Faivre et al. 2003a, Alonso-Alvarez et al. 2004, Peters et al. 2004a, Gautier et al. 2008, Rosenthal et al. 2012; but see Velando et al. 2014). Carotenoid bare parts may respond rapidly (within 6.5 hr) to stressors, including capture and captivity (Rosen and Tarvin 2006, Biard et al. 2009, Sternalski et al. 2010, Rosenthal et al. 2012, Vergara et al. 2015), and their color reflects indices of recent stress such as corticosterone levels or the heterophil:lymphocyte ratio (Roberts et al. 2007, Pérez-Rodríguez and Viñuela 2008, López et al. 2011, Kelly et al. 2012). Carotenoid coloration also predicts the strength of individual immune responses and the ability to clear parasite infections (Faivre et al. 2003b, Peters et al. 2004b, Dawson and Bortolotti 2006, Velando et al. 2006, Stirnemann et al. 2009).

Social Influences

In addition to physiological condition, bare parts can respond to changes in social status or breeding condition (Gautier et al. 2008, Karubian 2008, Karubian et al. 2011,

Dey et al. 2014). Changes in response to the social environment are likely to be mediated by androgens, as suggested by the fact that circulating testosterone is correlated with melanin, carotenoid, and structural bare-part color as well as fleshy structure size (Zuk et al. 1995a, McGraw and Parker 2006, Laucht et al. 2010, Lahaye et al. 2014). For instance, male Zebra Finches increase the redness of their bills within 3 wk in the presence of females (Gautier et al. 2008). Among Red Junglefowl (*Gallus gallus*), dominant males increase in comb size within 2–3 wk of forming flocks with females, while subordinate males decrease in comb size (Zuk and Johnsen 2000, Cornwallis and Birkhead 2008). The effects of testosterone on both carotenoid coloration and fleshy bare-part size appear to be mediated by the downstream metabolite dihydrotestosterone but not by estradiol (Casagrande et al. 2011, 2012); however, males and females can show similar responses to testosterone implantation (Eens et al. 2000).

The rapid color changes observed via hemoglobin flushing are typically associated with social interactions. For example, Crested Caracaras (*Caracara cheriway*) and Lappet-faced Vultures (*Torgos tracheliotos*) use hemoglobin flushing during agonistic interactions over carcasses (Bamford et al. 2010, Dwyer 2014). Changes in skin turgidity on a similar timescale in hornbills and turkeys might also be associated with social situations (Buchholz 1995, Curio 2004). However, little is known about the condition dependence of such structures.

Genetic and Early-environmental Influences

In addition to reflecting current condition or status, bare parts can also provide information about intrinsic quality. In Zebra Finches, one study found that approximately 61% of the variability in bill color in adults was fixed, of which 42% was genetic and 19% early-environmental, while 39% of the variability was due to current environmental inputs (Schielzeth et al. 2012). Other estimates also support a narrow-sense heritability of approximately $h^2 = 0.4$ for carotenoid bare-part coloration (Price and Burley 1993, Price 1996, Bolund et al. 2010, Schielzeth et al. 2012, Vergara et al. 2015). For example, Zebra Finches show genetic variation in bill color that is cytoplasmically inherited (Evans et al. 2014) as well as color variation linked to the W-chromosome (Schielzeth et al. 2012, Evans et al. 2014), Z-chromosome (Husby et al. 2012), and 4 autosomes (Schielzeth et al. 2012). In Red Junglefowl and their domesticated descendants, comb size is partially controlled by genes on chromosome 3 in both sexes as well as by 2 genes on chromosome 1 that only influence expression in females (Wright et al. 2008). The genes on chromosome 1 appear to be linked with others related to female reproductive investment (Wright et al. 2008), suggesting that female comb size is a signal of inherent fecundity, which may explain why males invest more

sperm in females with larger combs (Cornwallis and Birkhead 2007a, 2008). The lengths of wattles, snoods, and spurs are related to specific alleles of the major histocompatibility complex, which suggests that they can convey genetic parasite resistance (von Schantz et al. 1996, Buchholz et al. 2004, Baratti et al. 2010).

Maternal effects can influence bare-part coloration; for example, yolk carotenoid levels are correlated with offspring leg color in Domestic Chickens (Koutsos et al. 2003). Yolk testosterone, however, has not been found to enhance carotenoid bare-part color (Rubolini et al. 2006, Müller and Eens 2009). There are also environmental influences in early development that carry over to adult bare-part carotenoid coloration and fleshy bare-part size, such as nutrition, stress, and parasitism (Zuk et al. 1990a, 1998, Ohlsson et al. 2003, McGraw et al. 2005, Schielzeth et al. 2012, Fairhurst et al. 2015). However, a detailed series of studies on Mallards (*Anas platyrhynchos*) found no impact of carotenoid supplementation or immune challenges in early life on adult bill color (Butler and McGraw 2012a, 2012b, 2013a, 2013b). The influence of genetics, the early environment, and current condition in shaping signal values represents an area that would particularly benefit from additional research, given the relatively limited understanding we currently have of gene-by-environment interactions.

The Influence of Age

Melanin, carotenoid, and structural colors in bare parts can all change predictibly with age (Buchholz 1995, Bortolotti et al. 1996, Negro et al. 1998, Fenoglio et al. 2002, Curio 2004, Nicolaus et al. 2007, Vergara et al. 2015), though caution is needed when aging birds by bare-part color, given its flexibility (O'Donoghue et al. 1998, Sellers 2009). Signals of age may serve as de facto signals of quality, because older individuals are those that have survived longest (Andersson 1994, Buchholz 1995), although ornament expression can decline with age as well. In male Blue-footed Boobies and Zebra Finches, carotenoid-based bare-part color declines in senescence, and older birds show a greater decline in color following an immune challenge (Torres and Velando 2007, Cote et al. 2010, Simons et al. 2016). However, under carotenoid supplementation, older male Blue-footed Boobies actually increase foot coloration more than younger ones, perhaps trading off somatic maintenance for enhanced reproduction in what may be their last breeding attempt (Beamonte-Barrientos et al. 2014). Although color is negatively correlated with the number of previous breeding attempts in Blue-footed Boobies, males can enhance their foot color for the next season by skipping a breeding attempt (Velando et al. 2010), which indicates that older males might use "sabbaticals" to maintain ornament expression. In Red Junglefowl, a much shorter-

lived, polygynous species, individual male comb size does not decline with age, but the most ornamented males die younger, leading to decreasing average comb size with age (Cornwallis et al. 2014). Females, by contrast, show the greatest individual and average comb size in midlife. In Red-legged Partridges (*Alectoris rufa*), older males show a depressed response to testosterone and do not elevate carotenoid-based leg color as young males do (Alonso-Alvarez et al. 2009). Taken together, these studies indicate that older male birds have difficulty maintaining bare-part expression but may have strategies to balance the costs of ornamentation in different situations to maximize fitness.

FUNCTIONS OF BARE PARTS

Bare parts are used in a diverse range of signaling contexts, consistent with a function in social selection whereby signals mediate competition for resources, including mates (West-Eberhard 1979, Lyon and Montgomerie 2012). Social selection may be a more useful framework for interpreting bare-part signals than sexual selection per se, because many bare parts may be used in both sexual and nonsexual contexts. For instance, some colorful bare parts are maintained outside of the breeding season when they may be helpful in facilitating competition over food, territories, and other resources that indirectly affect breeding success. The few studies conducted outside of the breeding season suggest that bare parts may actually be more variable at this time and that relationships with condition could be heightened. Males are more variable in their androgen levels and ornament expression when not breeding, and uniformly high androgens for breeding can erase variability and obscure relationships with ornaments (Papeschi et al. 2000, Laucht et al. 2010). In addition, greater environmental stress in winter contributes to greater variability in the maintenance of ornamentation (Shirley et al. 2003). While social interaction may be less intense outside of the breeding season for some birds, others become more gregarious in the winter, allowing for more intense social competition (Grzybowski 1983).

In a comparative study of passerines, Dey et al. (2015) reported that bill color is unrelated to sexual size dimorphism, unlike plumage color (Badyaev and Hill 2000), and that there is no relationship between bill color and plumage dichromatism. Dichromatism in the bill was also not related to indicators of sexual selection. Instead, bill color was related to measures of sociality, such as coloniality and nonbreeding-season gregariousness. This led Dey et al. (2015) to suggest that bare parts did not originally evolve as sexual signals. Olson and Owens (2005) found that coloniality was a stronger predictor of bare-part color than plumage color across birds, supporting the idea that bare parts are used in a variety of social conflicts over resources other than mates. However, there were also

indications that carotenoid bare-part color is associated with polygamy, and many bare parts are certainly used in mate choice (discussed below).

Overall, our review indicates that studies more frequently find support for the role of bare parts in intrasexual competitive interactions (78% of studies, $n = 32$), typically over mates, than in intersexual mate choice (62% of studies, $n = 68$), though both functions appear to be common and are not mutually exclusive. However, phylogenetically controlled comparative studies like those cited above are rare, and we lack a basic understanding of how the distribution of bare-part color across birds is related to social and ecological conditions. Future comparative studies should assess how different types of coloration and different bare parts (i.e. bills vs. legs) vary in relation to social organization and breeding system as well as environmental parameters, while controlling for phylogeny.

Viability Selection on Bare Parts

Although many studies have found bare parts to be condition-dependent signals, there are also examples of color patterns that appear to be driven by nonsocial natural selection. Melanin in the dorsal maxilla of birds can reduce glare (Burtt 1984), and dark maxillary coloration may be more common in aerial insectivores and birds that forage in bright, open places (Williams and Burtt 2010). Selective pressures such as these may have provided the original purpose for melanic bill color, which could then have been co-opted as a social signal of testosterone levels. Melanin is also known to give strength and durability to feathers (Burtt 1986, Kose and Møller 1999). One study found that European Starling bills are harder and more resistant to abrasion when melanized (Bonser and Witter 1993); the authors proposed that this may explain the pattern of seasonal color change in European Starling bills, with breeding-season yellow being replaced with black for winter, when bills are subjected to greater forces in feeding. The replacement of melanin by carotenoids in the breeding season may impose a cost on males in terms of bill strength, enforcing the honesty of the signal, which explains why the bill tip is the last part to be de-melanized (Wydoski 1964). The relative strength of opposing pressures of sexual selection in the breeding season and natural selection in the nonbreeding season may be responsible for the seasonality of many nuptial colors. For instance, in Dusky Moorhens (*Gallinula tenebrosa*), individuals that have retained breeding colors into the winter are more often found at sites with better habitat quality and higher minimum temperatures (Shirley et al. 2003), implying a fitness cost to maintaining carotenoid ornaments through the nonbreeding season. In European Starlings, as well, populations living in milder climates gain breeding bill color earlier (Wydoski 1964).

An experiment on male Zebra Finches showed that cold temperatures reduce bill color within 2 wk, an effect than can be alleviated by carotenoid supplementation (Eraud et al. 2007).

Among the wood-warblers (Parulidae), melanin in the legs appears to be an adaptation to reduce radiant heat loss to the environment. Species that spend more time on their wintering grounds and experience lower annual minimum temperatures have darker legs (Burtt 1986). Thermoregulation also provides an explanation for hemoglobin-flushing. Many large, dark-bodied birds have extensive patches of bare skin on the head and neck with a higher density of blood vessels than the surrounding feathered skin (Negro et al. 2006). These patches, along with bare legs and feet, allow birds to disperse excess heat (Kahl 1963, Phillips and Sanborn 1994, Buchholz 1996). Hemoglobin-flushing for thermoregulation causes a change in skin color that could have subsequently been selected for a signaling function in some species (e.g., *Caracara* spp.; Negro et al. 2006). In addition, the casques of Southern Cassowaries (*Casuarius casuarius*; Phillips and Sanborn 1994) and Helmeted Guineafowl (*Numida meleagris*; Crowe and Crowe 1979), and the bills of Toco Toucans (*Ramphastos toco*; Tattersall et al. 2009) and Southern Yellow-billed Hornbills (*Tockus leucomelas*; van de Ven et al. 2016), may all play a thermoregulatory role without noted color change, though the pigments found in these structures might influence thermoregulation. Among the Phasianidae, fleshy structures are more common, larger, less sexually dimorphic, and more likely to be extended outside of display contexts in species living at lower latitudes, which suggests that thermoregulation is a function of these structures in hot climates and that heat loss may constrain display evolution in colder climates (Buchholz 1994). The ancestor of the Phasianidae likely had monomorphic fleshy structures for thermoregulation that were subsequently elaborated via sexual selection in some species (Kimball and Braun 2008, Kimball et al. 2011). The ability to erect and contract wattles is a synapomorphy of the core phasianids ("erectile clade") and could have originally evolved to aid in thermoregulation or display or to protect the wattles in combat (Kimball and Braun 2008).

Bare Parts in Competitive Interactions

Competition may be the primary social context in which bare parts are evaluated by conspecifics. Among studies of dominance, aggression, and territoriality ($n = 32$), 75% of studies found support for the importance of bare-part color or size in competitive interactions, 22% found no support for this role, and 3% found mixed support. Taken together, these results indicate that 20 of the 23 species studied (87% of species) are likely to use bare parts to mediate intrasexual conflict. Apart from the spurs of

certain phasianids, bare parts are typically not considered weapons (*sensu* McCullough et al. 2016), although in many species bills are used in aggressive encounters. More commonly, bare parts appear to function as "pure" signals, which convey either willingness to compete for resources or aspects of condition that may convey information about competitive ability. Species with rapid, behavioral bare-part signals seem to use them mainly in an aggressive context, such as flushing by Crested Caracaras and Lappet-faced Vultures in agonistic interactions over carcasses (Bamford et al. 2010, Dwyer 2014). Carotenoid bare-part color is linked to aggression and dominance as well (Miskelly 1981, Shawcross and Slater 1984, Murphy et al. 2009, Ardia et al. 2010). For example, bill color predicts aggressiveness in Zebra Finches and is associated with dominance among males when they are allowed to interact over time and form natural hierarchies. A testosterone injection increases both bill redness and dominance score within 3 days (Ardia et al. 2010). Interestingly, in one-off interactions in which males do not have time to form hierarchies, bill color does not predict aggression or dominance (Etman et al. 2001, Bolund et al. 2007). By contrast, bill color mediates dominance interactions among female, but not male, American Goldfinches (Murphy et al. 2009, 2014). Bill color not only shapes the outcome of these interactions but responds to it, with color increasing in winners and decreasing in losers (Tarvin et al. 2016). Additionally, it appears that social interactions could possibly have such a strong influence on bare-part color that it obscures relationships with condition. In the study above, the bill color of female American Goldfinches reflected the outcome of competitive interactions but not induced energetic stress, despite the existence of a correlation between carotenoid-based bare-part color and the same stress indicators in other species (Pérez-Rodríguez and Viñuela 2008, López et al. 2011, Svobodová et al. 2013).

No studies have attempted to explicitly link melanin in bare parts to aggression or dominance, but black bill color is linked to testosterone expression in House Sparrows and Red-backed Fairywrens (*Malurus melanocephalus*; Laucht et al. 2010, Karubian et al. 2011). In the families Phasianidae and Rallidae, comb and wattle size predicts the outcome of dominance interactions (Allee et al. 1939, Collias 1943, Gullion 1951, Gjesdal 1977, Moss et al. 1979, Holder and Montgomerie 1993, Buchholz 1997, Mateos and Carranza 1997, Zuk and Johnsen 2000, Dey et al. 2014). In male Red Junglefowl, comb size increases within 2 wk when males become dominant and decreases when they become subordinate (Zuk and Johnsen 2000, Cornwallis and Birkhead 2008). As in Zebra Finches, signal expression before males interact does not necessarily predict dominance; rather, it is after males have been allowed to interact that the signal changes to reflect status.

In the Australian Swamphen (*Porphyrio melanotus*), experimental alteration of the frontal shield to appear smaller results in increased aggression against the treatment individual. This, in turn, causes actual shield size to decrease within 1 wk (Dey et al. 2014), demonstrating how bare parts are subject to dynamic feedback with the social environment.

Mate Choice for Bare Parts

Mate choice is one of the most common contexts in which bare parts are studied. Among studies of mate choice ($n = 68$), 51% of studies supported the importance of bare-part color or size in mate choice, 38% found no support for this role, and 11% found mixed support. Taken together, these results indicate that 22 of the 29 species studied (76% of species) are likely to evaluate bare parts in mate choice. Some species mate assortatively by bare-part color (Jawor et al. 2003, Massaro et al. 2003, Møller et al. 2007, Parker 2014, Vergara et al. 2015; but see Van Rooij and Griffith 2012); in other species, individuals with brighter bare parts are mated to partners in better condition (Faivre et al. 2001, Torres and Velando 2003, Vergara et al. 2011). For example, in Mallards, males with brighter bills have higher pairing success (Omland 1996a, 1996b). In Wattled Jacanas (*Jacana jacana*) and Black Kites (*Milvus migrans*), individuals with a breeding territory display more saturated bare parts than floaters (Emlen and Wrege 2004, Blas et al. 2013). Among the polygynous Phasianidae, the color and size of male combs and wattles are often correlated with success in achieving copulations (Brodsky 1988, Zuk et al. 1990b, Buchholz 1995, Zuk et al. 1995a, Bart and Earnst 1999, Rintamäki et al. 2000, Parker and Ligon 2003; but see Siitari et al. 2007). However, in many phasianids, there are 2 components of the display: the erection of the wattles, which conveys territorial status or dominance, and the actual properties of the wattles that females might assess (Kimball and Braun 2008). In Ring-necked Pheasants (*Phasianus colchicus*), erection of the wattles obscures differences in their size, so females instead rely on the size of the feathered ear tuft, which is static and correlates with the size of the unerected wattle (Mateos and Carranza 1995, Mateos 1998). This illustrates how mating success by ornamented males does not always imply female choice for ornamentation. In frigatebirds (*Fregata*), for instance, although courting males increase their gular pouch redness (Madsen et al. 2007b), multiple studies have failed to find any link between female choice and the color or size of the pouch (Dearborn and Ryan 2002, Madsen et al. 2007a, 2007b, Wright and Dearborn 2009, Juola 2010).

More direct confirmation of a role for bare parts in female mate choice comes from experimental manipulations. In Zebra Finches and Least Auklets (*Aethia*

pusilla), females preferentially associate with models or live males that have artificially enhanced bill color (Burley and Coopersmith 1987, Jones and Montgomerie 1992, Sullivan 1994a, de Kogel and Prijs 1996). In King Penguins, reduction of the UV signal of the bill spot causes individuals to have more difficulty pairing (Nolan et al. 2010). Although some studies have found no link between bill color and mate choice in Zebra Finches (Collins et al. 1994, Forstmeier and Birkhead 2004, Bolund et al. 2007, Schuett et al. 2011, Tschirren et al. 2012), reviews and meta-analyses suggest that females exhibit preferences for natural variation in bill color when selecting mates (Collins and ten Cate 1996, Simons and Verhulst 2011). Some of the confusion may have arisen from the fact that male Zebra Finches can up-regulate their bill color within 3 wk when kept with females (Gautier et al. 2008). In Red Junglefowl, meta-analysis of experimental manipulations shows that females prefer males with larger and more colorful combs (Parker and Ligon 2003), whereas males use female comb size to make decisions about sperm allocation (Cornwallis and Birkhead 2007a, 2008). Bare parts can also influence extrapair copulations: In Zebra Finches and Blue-footed Boobies, females are more likely to mate with an extrapair male if his bare-part color is brighter than that of her social mate (Houtman 1992, Kiere and Drummond 2014; but see Tschirren et al. 2012).

Ontogenetic changes in the timing of bare-part color expression also point to a signaling role in mate choice. Changes in the color or growth of bare parts are often associated with sexual maturity, and sex differences in bare-part color may not be apparent in juveniles (Casagrande et al. 2007). Among adults, bare parts typically grow more colorful as the breeding season approaches and then fade after pairing and laying (Burley et al. 1992, Jones and Montgomerie 1992, Negro et al. 1998, Heath and Frederick 2006, Madsen et al. 2007b, Pérez et al. 2008, Pérez-Rodriguez 2008, Laucht et al. 2010, Karubian et al. 2011). For example, in male American Kestrels (*Falco sparverius*), plasma carotenoids and bare-part color are both at their highest during pair formation but then fall during incubation and rearing, reaching the level of females and nonbreeding males (Negro et al. 1998). In Zebra Finches, bill color increases prior to breeding in both sexes, dulls during incubation, and increases again when reproductive effort is suspended (Burley et al. 1992). While the acquisition of nuptial plumage is dependent on luteinizing hormone in many passerines (Kimball and Ligon 1999), acquisition of nuptial bill color instead appears to be controlled by testosterone and estrogen (Witschi 1935, Mundinger 1972); however, seasonal changes in bill color may be attributable to complex interactions between sex hormones and gonadotropins (Lofts et al. 1973). Fleshy bare parts, dependent on

testosterone, also increase in size as breeding approaches (Young 1970, Visser 1988, Zuk et al. 1990a, 1990b).

Patterns of bare-part expression within and among some species appear to be consistent with a signaling role in mate choice or intrasexual competition over mates. Many studies report that bill color is typically brighter or more saturated in the sex with the more ornamented plumage (Alonso-Alvarez et al. 2004, Kelly et al. 2012, Walsh et al. 2012, Cardoso et al. 2014, Vergara et al. 2015). In birds with sexually monochromatic plumage, males and females often have monochromatic bare parts (Eens et al. 2000, Velando et al. 2001, Massaro et al. 2003, Jouventin et al. 2005, Stirnemann et al. 2009, Doutrelant et al. 2013). In the sex-role-reversed Wattled Jacana, bare parts are brighter in females, the mate-limited sex (Emlen and Wrege 2004). Dey et al. (2015) found no relationship between bill color and indicators of sexual selection in passerines, but they and others scored bill color on the basis of plates and thereby may have missed subtle sexual dichromatism in bill color that could have been detected with a photospectrometer. Relatively fine-grained, longitudinal studies of color-marked individuals to document variation across sex, age, and season will provide new insights into patterns of bare-part coloration and signal potential.

Reproductive Investment in Response to Bare Parts

Reproductive investment decisions in response to the bare-part signals of a partner have been observed in many species. For example, in boobies (*Sula* spp.), females alter their investment by reducing egg size in response to experimental reductions of male bare-part color (Velando et al. 2006, Montoya and Torres 2015). Differential female investment in response to variation in male bare-part color has also been observed in Red-legged Partridges (Pérez-Rodríguez and Viñuela 2008, Alonso-Alvarez et al. 2012), Eurasian Kestrels (*F. tinnunculus*; Vergara and Fargallo 2011), Common Blackbirds (Faivre et al. 2001, Préault et al. 2005), Zebra Finches (Gil et al. 1999), and Mallards (Giraudeau et al. 2011). Changes in female investment include changes in clutch size and lay date (Pérez-Rodríguez and Viñuela 2008, Vergara and Fargallo 2011); in yolk properties, including weight, carotenoids, androgens, and lysozyme concentration (Gil et al. 1999, Alonso-Alvarez et al. 2012; but see Zanollo et al. 2013); and in nest visitation (Faivre et al. 2001, Préault et al. 2005). Males can also adjust parental care (Morales et al. 2012) or sperm quantity and quality (Cornwallis and Birkhead 2007a, 2007b) in relation to variation in female bare-part ornaments.

The differential allocation hypothesis proposes that individuals should adjust their own investment in relation to the attractiveness of their mate (Burley 1986, Sheldon 2000). The previous examples demonstrated positive

differential allocation (Ratikainen and Kokko 2010), in which partners increase investment when their mate is more attractive. Several studies have shown that males with brighter bare parts provision the nest more (Casagrande et al. 2006, Montoya and Torres 2015) and fledge more young (Préault et al. 2005, Leclaire et al. 2011), so it should be advantageous for females to continuously evaluate male bare parts and adjust their own investment accordingly. However, other responses to mate phenotype are possible, such as negative differential allocation (decreasing investment with more attractive mates) and the related idea of reproductive compensation (investing more to compensate for expected offspring deficiencies; Gowaty et al. 2007, Ratikainen and Kokko 2010). The results of a study of Blue-footed Boobies in which foot color influenced mate choice in both sexes (Torres and Velando 2005) indicate that the influence of bare-part color on investment is conditioned by other cues of partner quality. Male incubation effort was positively related to female foot color when the female's eggs were small; however, when eggs were large the relationship was reversed, with males providing more effort to females with duller feet. Males may have perceived that a female with large eggs and dull feet had sacrificed her own condition for fecundity (Fitzpatrick et al. 1995), and thus they increased their own investment to compensate for their partner's poor condition (Morales et al. 2012). Positive differential allocation is more common overall in nature (Horváthová et al. 2012), and models indicate that negative differential allocation should occur only in narrow circumstances; these include cases in which individuals have high energy reserves, investment in offspring is not very costly, or individuals face limited prospects for future reproductive success (Harris and Uller 2009). Because birds are iteroparous organisms that may reproduce many times, often with the same mate, partnerships with large asymmetries of quality or effort are unlikely to be repeated in subsequent years. Bare parts offer birds the flexibility to alter investment decisions not just with different partners but with the same partner, within one breeding season, as new information becomes available.

Nestling Signals and Parental Investment

In many bird species, social signaling begins immediately after hatching, in the context of parent–offspring conflict and sibling competition. Carotenoids in the mouths of nestlings can reflect diet (Ewen et al. 2008, Thorogood et al. 2008), immune status (Saino et al. 2003), body condition (Jacob et al. 2011), and corticosterone levels (Loiseau et al. 2008). Many nestling birds have also evolved a bright flange to the gape, which may serve to increase detectability and can be a condition-dependent signal itself (Kilner and Davies 1998, Dugas and Rosenthal 2010, Jacob et al. 2011). For example, in chicks of Barn Swallows

(*Hirundo rustica*), carotenoid coloration in the gape conveys current infection status while the UV signal of the gape flanges reflects chick size and weight gain (Saino et al. 2000, de Ayala et al. 2007). In this species and several others, parents preferentially feed chicks that signal good health (Götmark and Ahlström 1997, Loiseau et al. 2008, Dugas 2009), but they may also allocate food to nestlings that are in worse condition (Parejo et al. 2010). In Island Canaries (*Serinus canaria*) and other seed-regurgitating finches, chicks flush hemoglobin through their gapes when hungry, signaling their need and eliciting feeding (Kilner 1997, Kilner and Davies 1998). Across species, the redness of the gape increases with the degree of extrapair paternity in clutches, and cuckoos tend to have redder gapes than their hosts, both indicating that sibling competition is a driver of gape coloration (Kilner 1999). These patterns hold only for species that build open nests with enough light to discriminate color (Kilner 1999).

Juvenile birds can also convey condition via leg coloration, as in storks and raptors (Negro et al. 2000, Casagrande et al. 2009, Sternalski et al. 2010), and the UV reflectance of nestling skin appears to be a signal that influences parental feeding (Jourdie et al. 2004, Bize et al. 2006). Juvenile American Coots (*Fulica americana*) display bright red skin on their head as well as orange feathers, which both appear to have evolved via parental favoritism for colorful chicks (Lyon et al. 1994). Among the rallids, such chick "ornamentation," including colorful bills and skin patches, is associated with polygamy and large clutches, again implicating sibling competition as a driver of coloration (Krebs and Putland 2004). Bare-part coloration may also play a role in interactions between individuals of different age classes. For example, in Common Blackbirds, juveniles avoid intrasexual aggression from adults by displaying a dull, female-like bill (Préault et al. 2005). Bare parts in young birds of some species might also be under sexual selection already; for instance, in Bearded Reedlings (*Panurus biarmicus*), pair formation begins before plumage is mature, but when birds already display sexually dimorphic carotenoid-based bill color (Surmacki et al. 2015). Parents can also use bare parts to signal to their offspring, as in many gulls in which bill color directs the nestlings to peck for food (Tinbergen and Perdeck 1950, Collias and Collias 1957, Velando et al. 2013). The size of the red bill-spot is condition dependent and is also gauged by partners to determine their own optimal level of investment (Morales et al. 2009a, Pérez et al. 2010a, 2010b).

BARE PARTS AND PLUMAGE AS MULTIPLE ORNAMENTS

A number of hypotheses have been proposed to explain the existence of multiple ornaments (Møller and Pomian-

kowski 1993, Candolin 2003, Hebets and Papaj 2005). Multiple ornaments could convey the same signal but provide a backup against signal error or environmental noise (Møller and Pomiankowski 1993, Hebets and Papaj 2005). Alternatively, they could convey different signals to the same receiver or be targeted at different receivers (Møller and Pomiankowski 1993, Andersson et al. 2002). There may also be emergent properties of multiple signals; for instance, the difficulty of producing several signals in different modalities may itself convey an individual's ability to expend resources on multiple tasks simultaneously (Hebets and Papaj 2005). Bare-part color has often been analyzed along with various plumage traits of similar color, as if it represented simply one more characteristic of the same overall signal. However, under a systems theoretical approach to animal communication (Hebets et al. 2016), the different structures of feathers and the dermis indicate that, at the very least, bare parts and plumage represent *degenerate* signals (different structure, same function) rather than truly *redundant* signals (same structure, same function). This distinction is important, because degenerate signals can respond independently to selection and give a system greater robustness and functionality (Hebets et al. 2016).

Møller and Pomiankowski (1993) first argued that signals with different phenologies—such as those that are static vs. those that change over short periods—should be considered multiple messages. The ability of bare parts to respond relatively rapidly to changes in condition, environment, or status presents a striking contrast with plumage, which is thought to be a relatively static signal because it depends on annual or semiannual molt cycles for replacement (but see Lantz and Karubian 2016). Plumage is likely to reflect average condition over a relatively long period (the period during which feather growth occurs), whereas bare parts can provide flexible, up-to-date information on current condition or status that changes within days, hours, or even seconds. Bare parts are well suited to reflect changes in breeding status in cooperatively breeding species, in which individuals may move from nonbreeding auxiliary helpers to breeders as quickly as a vacancy occurs. In Red-backed Fairywrens, for example, drab nonbreeding males can rapidly gain the black bill color of breeding males when a breeding vacancy opens, signaling their change in status (Karubian 2008, Karubian et al. 2011). Similarly, male Zebra Finches will up-regulate their bill color in the presence of females (Gautier et al. 2008). Among group-living or highly social species that maintain dominance hierarchies, bare-part signals are better suited for indicating changes in social status year round than plumage-based signals, which might take months to reflect a change in status.

Despite the shared use of carotenoids, melanin, and structural colors in both plumage and bare parts, one cannot assume that the relationships between coloration and condition are identical in the 2 types of ornaments. For instance, dietary limitation and physiological trade-offs are typically invoked to explain the honesty of carotenoid-based signals, yet carotenoids appear to be less limiting for bare parts than for plumage. Diet is a better predictor of plumage color than bare-part color across species (Olson and Owens 2005); and gut parasites, which inhibit the absorption of carotenoids and the production of lipoproteins (Allen 1987), appear to have a relatively more severe impact on plumage (Hatchwell et al. 2001, Mougeot et al. 2005, 2007b, Biard et al. 2010, Martínez-Padilla et al. 2010, López et al. 2011). Because many bare parts occupy a small surface area in relation to plumage ornaments, they may require fewer carotenoids to color. For this reason, some species, such as large birds with carotenoid-poor diets, may lack sufficient plasma carotenoids to support coloring plumage (Tella et al. 2004) but have ample levels to support coloring of bare parts. For example, phasianids tend to circulate plasma carotenoids at a concentration 1–2 orders of magnitude lower than that of fringillid and estrildid finches (McGraw 2005), and only the latter display carotenoids in feathers. Unlike for plumage (Tella et al. 2004), there is no relationship between body size and bill coloration (Dey et al. 2015), at least in the passerines. Across 140 families, total egg clutch mass is negatively related to carotenoid color in plumage but not in bare parts (Olson and Owens 2005), possibly indicating that, for females, a trade-off between signaling and offspring investment exists for plumage but not for bare parts. These constraints could help explain why carotenoid coloration in bare parts is more common and evenly distributed across families (Olson and Owens 2005) and why it is observed in taxa that appear to lack feather carotenoids, such as raptors, seabirds, and ground-birds.

In 3 species with plumage and bare parts of the same pigment class—American Goldfinches and Northern Cardinals (*Cardinalis cardinalis*) with carotenoids, and House Sparrows with melanin—researchers have investigated the condition dependence of both ornaments. Results suggest that bare-part and plumage color are not correlated with one another, and that plumage color may better reflect aspects of quality with a stronger genetic component such as metabolic rate, allelic diversity, and body size (Jawor and Breitwisch 2004, Rosen and Tarvin 2006, Václav 2006, Laucht et al. 2010, Kelly et al. 2012, Laucht and Dale 2012), whereas bare-part color better reflects more environmentally influenced traits such as acquired immunity, body condition, current hormone levels, and recent stress (Jawor and Breitwisch 2004, Hill et al. 2009, Laucht et al. 2010, Kelly et al. 2012). In American Goldfinches, plumage color but not bill color reflects current *Trypanosoma* load (Lumpkin et al. 2014); however, in general, bare parts are unreliable signals of the

chronic, low-level endoparasite infections common to many birds (Hatchwell et al. 2001, Mougeot and Redpath 2004, Mougeot et al. 2005, 2007b, Biard et al. 2010, López et al. 2011), indicating that chronic infection severity reflects the innate immunocompetence of individuals rather than posing an acute immune challenge that would be reflected in bare-part color. Some have noted that studies of bare parts find stronger support than studies of plumage for a direct trade-off of carotenoids between signaling and immunity (Hill 2006) and for a link between color and oxidative stress (Hill et al. 2009). These patterns are consistent with a long-standing but rarely tested hypothesis: that static or fixed signals are more reliable signals of genetic quality because they integrate condition over a longer period and are relatively unaffected by short-term fluctuations (Sullivan 1994b, Candolin 2003, Scheuber et al. 2004, Hebets and Papaj 2005). This hypothesis can be explicitly tested by performing heritability analyses on bare parts and plumage of the same color in the same species. Currently, evidence is insufficient to say whether one is consistently more heritable than the other (Price and Burley 1993, Price 1996, Mundy 2006, Quesada and Senar 2009, Bolund et al. 2010, Evans and Sheldon 2012, Schielzeth et al. 2012, Vergara et al. 2015). We also need to better understand the relative contributions that genetics, the early environment, and current condition make to variation in both bare parts and plumage.

If bare parts and plumage are uncorrelated and convey multiple messages, we should expect them to be evaluated differently by receivers, and the few studies conducted thus far have found some support for this. For example, Northern Cardinals mate assortatively by both red plumage color and red bill color, with a slightly stronger effect for plumage (Jawor et al. 2003). In females, red plumage color but not bill color predicts reproductive success (Jawor et al. 2004), though in males neither does (Jawor and Breitwisch 2004). In Common Waxbills (*Estrilda astrild*), which also have red bills and plumage, both sexes make intersexual and intrasexual preferential associations based on plumage color but not bill color (Cardoso et al. 2014). Future studies should experimentally manipulate either bare-part or plumage color while holding the other constant and evaluate the response in terms of social dominance or attractiveness to mates.

THE IMPORTANCE OF AVIAN BARE PARTS AS SIGNALS

We found evidence that bare parts may be used as flexible, condition-dependent social signals across diverse avian taxa. This claim is based on the fact that both the color and size of bare parts respond in predictable ways to changes in the social or physical environment, and that diverse receivers modify their behavior in response to these changes. Bare parts often reflect current condition or health and can also convey information about intrinsic quality as determined by genetics and the early environment. Receivers can use these signals to make choices about competition, mating, reproductive investment, and allocation of resources to offspring.

Bare-part signals are likely to occupy a signaling niche distinct from that of both plumage and vocalizations. For instance, their relative inconspicuousness probably makes bare parts most effective at close range. Unlike in plumage, patterning is almost entirely absent from bare parts, making them poor signals of individual identity as well. Instead they may be more accurately viewed as pluripotent social signals of condition, reflecting a variety of different socio-environmental inputs on relatively short timescales. More than anything, they resemble the flexible color signals found in fishes. Fish integument is studded with melanophores and chromatophores, pigment-containing cells that in some species can change color in seconds by moving pigment around (an avian analogue would be hemoglobin flushing). However, the number of these chromatophores is also plastic, leading to interindividual variation in baseline coloration that closely resembles the flexibile condition dependence of most bare-part signals (Kodric-Brown 1998, Sköld et al. 2016). In fishes, carotenoid coloration varies in relation to diet, immune stress, hormones, and condition and is evaluated by both mates and competitors (Kodric-Brown 1985, 1998, Sefc et al. 2014). Recently, Hutton et al. (2015) argued that dynamic color systems, particularly in cephalopods, teleostean fishes, and lizards, are open to the same conceptual and methodological approaches long applied to other dynamic behaviors such as displays or vocalizations. We believe that the literature on avian bare parts is sufficiently developed to make them a comparable taxon for the study of color dynamism. In addition, avian bare parts have been studied in diverse contexts, tying color change to a rich literature on immunology, parasitism, nutrition, development, competition, reproduction, and selection.

Bare parts are highly integrative signals, in that a variety of genetic, social, and environmental inputs of different magnitudes and directions are integrated into a simple signal that primarily varies along one axis, from dull to bright. Context should be important for the accurate evaluation of such a signal (e.g., Gillespie et al. 2014). Plumage might be one critical source of context for the accurate evaluation of bare-part signals, as a seasonally static background against which they can be compared. A bird with a dull bill but brilliant plumage might be a high-quality mate suffering from a temporary infection; a bird with the opposite condition might be a decent forager that survived scarcity during molt. Accurate evaluation of a flexible signal also requires assessing the signal over time (Sullivan 1990). For instance, in a study of Zebra Finches in

which the bill color of the same males was manipulated each day, females based their choice on the history of bill color rather than simply its present state (Sullivan 1994a). Given enough time, a receiver can form a more accurate perception of the signaler by integrating or averaging fluctuations in the signal (Sullivan 1994b); indeed, in Zebra Finches, bill color does not predict dominance until males have had the chance to interact over time and form stable hierarchies, and until, presumably, color in all of them has stabilized as well (Etman et al. 2001, Bolund et al. 2007, Gautier et al. 2008, Ardia et al. 2010). We should expect bare-part signals to evolve where individuals can recognize each other and interact repeatedly over time. In addition to exploring patterns of bare-part ornamentation in relation to social organization, future comparative studies could also examine the role of bare-part signals in different mating contexts such as monogamy, promiscuity, and lekking. It is possible that bare parts will be weighted more strongly in decisions regarding social mates, where individuals interact repeatedly and direct benefits are a consideration. Plumage, by contrast, may be more important in decisions about copulations or extrapair mates, where individuals might interact only once, and where indirect genetic benefits are likely to be paramount.

Some degree of bare-part color is often found in both sexes. Despite clear evidence that females display condition dependence in bare parts (Gladbach et al. 2010, Kelly et al. 2012, Rosenthal et al. 2012, Doutrelant et al. 2013) and use them for signaling (Nolan et al. 2010, Dey et al. 2014, Tarvin et al. 2016), there has been little study of female bare parts in relation to those of males. Females experience intrasexual competition largely for high-quality mates (Rosvall 2011), and their bare parts can play an important role in competitive interactions (Murphy et al. 2009) and male mate choice (Torres and Velando 2005, Cornwallis and Birkhead 2007a, 2007b). However, because females circulate fewer plasma carotenoids than males (Bortolotti et al. 1996), allocate some of their carotenoids to eggs (Negro et al. 1998, Blount et al. 2000, McGraw and Toomey 2010), and face selection for crypsis on the nest (Bortolotti 2006), some of their signals will be under constraints and trade-offs distinct from those of males. For instance, across species, colorful plumage is related to a decrease in egg mass, evidencing a trade-off, a relationship not seen for colorful bare parts (Olson and Owens 2005). Among dabbling duck species, gains in bill color are associated with the loss of showy plumage, which has been interpreted to mean that selection for crypsis favors bare parts over plumage signals for the same function (Johnson 1999). With their small surface area, bare parts may offer females a signal that is less costly to color and less conspicuous on the nest than bright plumage, and colorful bare parts are commonly observed in females that are otherwise drab. If bare-part signals are disproportionately common in females compared to plumage signals, a testable hypothesis, it may be indicative of evolutionary constraints on female ornamentation that are less severe for bare parts.

CONCLUSION

It is our hope that this review will cause ornithologists as well as evolutionary and behavioral ecologists to pay greater attention to the evaluation and interpretation of avian bare-part signals. Colorful bare parts are not equivalent to colorful feathers; rather, they represent a phenologically distinct set of tissues with a unique suite of signaling properties. The usefulness of flexible bare-part signals in conjunction with more static plumage-based signals for conveying a wider range of information may be one explanation for the evolution and maintenance of multiple ornamentation in birds. By better characterizing avian bare parts, we can develop a more inclusive theory of animal communication, one that emphasizes how temporally divergent signals complement and reinforce each other adaptively.

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