On the multifunctionality of feathers and the evolution of birds

Ryan S. Terrill[1] and Allison J. Shultz[2]

[1]Moore Lab of Zoology, Occidental College, 1600 Campus Rd. Los Angeles, CA 90042 USA

[2]Ornithology Department, Natural History Museum of Los Angeles County, 900 Exposition Blvd. Los Angeles, CA 90007 USA

*Correspondence: RST (ornithoterrill@gmail.com) and AJS (ashultz@nhm.org)

Abstract

The ability feathers have to perform many functions simultaneously and at different times is integral to the evolutionary history of all birds. Many studies focus on single functions of feathers; but any given feather performs many functions over its lifetime. Here, we review the known functions of feathers and discuss the interactions of these functions with avian evolution. Recent years have seen an increase in research on the evolution and development of feather functions because of an increase in high quality fossils with preserved feathers, new tools for understanding genetic mechanisms of feather development, new tools for measuring and analyzing feather color, availability of phylogenies and phylogenetic comparative methods, and an increase in interest in feather molt. Here, we aim to review how feather functions interact with avian evolution, with a focus on recent technological and discovery-based advances. By synthesizing research into feather functions over hierarchical scales, we aim to provide a broad context for how the adaptability and multifunctionality of feathers have allowed birds to diversify into the astounding array of environments and life-history strategies. Overall, we suggest research into avian evolution that involves feather function in any way should consider all aspects of a feathers’ functionality, including multiple functions, molt patterns, ecological/mechanical interactions, and feather wear over time. With this more holistic view,

processes such as the evolution of avian coloration and flight can be understood in a broader and more nuanced context.

1. Introduction

Feathers are unique among morphological traits in the variety of functions they perform, and this functional diversity enables the multifaceted life-histories birds currently employ. The structural, spatial, and temporal complexity of feathers provide a scaffold for selection to produce many different function phenotypes (Figure 1; Chen et al. 2015). Feathers are tubular epidermal beta-keratin structures found today only in birds, composed of a series of structures that add up to a single, complex structure (Figure 2). These hierarchical levels are detailed later in this paper, but vary in scale from shape and placement of whole feathers to the molecular structures that make up a single feather. The interactions of functions along these hierarchical levels largely determine the ability of feathers to perform multiple functions simultaneously (Figure 1).

The evolution of function in physical traits generally occurs through the incorporation of a novel function onto an existing trait, and feathers provide ample opportunities to study this phenomenon. For example, flight feathers that generate lift can become strengthened for use in bracing against vertical surfaces, become elongated to aid in abrupt aerial maneuvers, or become extremely elongated for sexual display. Body feathers that function for thermoregulation or waterproofing can incorporate bright colors for sexual signaling, or cryptic colors to help a bird blend in with its environment. In some cases, multiple separate functions are so fundamental to individual feathers that it can be difficult to determine which function may have evolved first. For example, body feathers that keep a bird warm and dry can help a bird hide from predators and prey through increased camouflage, or signal quality of a bird to potential mates. Which functions may have driven the origin of body plumage in early archosaurs may be difficult to ever know, although some research suggests visual signaling (Persons and Curie 2015) or protection from solar radiation (Regal 1975) may have played a more important role in the early evolution of feathers than previously thought. One seemingly clear statement that can be made on the functional origin of feathers is that feathers did not originally evolve for flight. Feathers are well-documented in fossils well before the origin of flight in avian progenitors, and both paleontological and molecular evidence agree that plumulaceous (non-flight) feathers preceded pennaceous (flight) feathers (Harris et al. 2005). This is a demonstrative example of the multiple functions of feathers: feathers evolve novel functions through modifications of the basic structure, and are often able to achieve these functions in a very efficient manner.

Here, we aim to combine a broad-scale understanding of how feathers function, a description of how these functions evolve and interact with the evolution and diversification of birds, and recent research on the evolution, genetics, and development of feathers. Additionally, we explore the consequences of multifunctionality in feather evolution. Because feathers are always performing multiple functions, the evolution of one function may be constrained or otherwise affected by any of its other functions. We explore how functions may interact within feathers over evolutionary time, and suggest ways that researchers should consider functional interactions within feathers when trying to understand feather evolution. We first explore individual functions of feathers, providing context for how a function is performed by the feather and example taxa that use feathers for each function. If there has been research into the evolutionary history or ecological interactions of a function, we explain these facets. Next, we explore the context for feather functions from an evolutionary perspective; specifically how the evolution of hierarchical structures of feathers, molt strategies, function interactions, and genetic and developmental bases of feather functions interact with feather functions. We emphasize the importance of multifunctionality of feathers and explain how multiple functions may coexist within an individual through variation in hierarchical structure and molt strategies, as well as the interplay of functions over evolutionary time through trade-offs associated with feather functions. This manuscript aims to serve as a reference for feather functions, as well as to explore the current knowledge of their evolution. We also identify gaps in the literature and make recommendations for future research directions into feather functions and their intersection with avian evolution.

2. Feather Functions

Feathers perform many functions for birds (Figure 3), and these multiple functions have allowed birds to adapt into novel and diverse lifestyles across the globe. The diversity of functions of feathers accompanies a related diversity in feathers structures (Prum 2005; Figure 1). These functions arise from modifications of a basic structural plan, specifically, changes in the shapes of structures in the feathers, color production mechanisms, and molting processes (Stettenheim 2000). Stettenheim (1976) reviewed these physical adaptations for separate functions and outlined many of the functions of feathers. Here, we expand upon that work by considering a number of functions he did not include, as well as updating knowledge of these functions in the context of locomotion, physiology, feeding, and communication, using contemporary literature review and including discussion of trait evolution and interactions with avian diversification.

Locomotion

Flight

Efficient flight has allowed birds to evolve diverse life-history strategies involving specialized flight, including annual long-distance migrations (Figure 3r) that cover most of the globe (Battley et al. 2012); dependence on extremely low-density and ephemeral food supplies in zones such as the desert and open ocean (Weimerskirch et al. 1993); foraging on fast, aerial prey such as arthropods (Figure 3q) and other birds (Rosen et al. 1999), and efficient locomotion for most non-cursorial feeding strategies (flying and swimming). Birds achieve powered flight and gliding through lift generated from the wings and tail (Maybury et al. 2001). The remiges, also known as flight feathers are the main load-bearing feathers in flight, and are articulated to bone to support the weight of a bird in flight. These feathers are also characterized by a thickened rachis relative to other feathers (Nudds and Dyke 2010) and a closed vane that is asymmetrical such that the anterior vane is smaller than the posterior vane (Feduccia and Tordoff 1979). The degree of asymmetry increases from the inner secondaries and rectrices (tail feathers), which are almost symmetrical, to the outer primaries and rectrices. In addition to the lift generated by these flight feathers, the wing coverts are layered on the wings to create an airfoil shape that creates lift on the wing during forward motion (Wang and Clarke 2015). All wing and tail feathers are layered with the proximal feathers to the body on top, with subsequently distal feathers below each proximal neighboring feather. The exception to this rule is the median secondary coverts, which layer in the opposite pattern, with the distal feathers on top. The origin and possible function of this reverse layering is unknown.

Flight feathers tend to be dark (Figure 3b) because melanin pigments that produce this dark color may strengthen feathers against degradation (Bonser 1995). Many white birds that spend significant time flying, such as the American White Pelican (*Pelecanus erythrorhynchos)*, White Stork (*Ciconia ciconia)*, or Snow Goose (*Anser caerulescens*), have black outer wing feathers. This pattern of dark outer flight feathers has been found in fossils, including *Archaeopteryx lithographica* (Carney et al. 2012) and other feathered dinosaurs (Li et al. 2014, Zhang et al. 2010). While historically the focus has been on melanin as a pigment that provides increased strength or resistance to degradation for feathers, recent research has also identified an additional possible function. Black wingtips on birds increase the immediate ambient temperature, reducing drag, and potentially aiding in flight efficiency (Rogalla et al. 2019).

The evolution of flight in birds has been a topic of interest and controversy since the discovery of the feathered Jurassic bird *Archaeopteryx lithographica* in 1861. Research suggests *Archaeopteryx* was capable of at least some powered flight (e.g. Nudds and Dyke 2010, Voeten et al. 2018); however, feathers likely evolved for some purpose other than flight (Feo et al. 2015, Lloyd et al. 2016) and were co-opted to serve as integuments for powered flight later in the evolutionary history of birds (Persons and Currie 2019). Despite the evolution of feathers predating that of flight, birds subsequently evolved numerous physiological adaptations for flight, and all crown birds descended from an ancestor that was highly adapted for flight (Padian et al. 1998).

Despite many benefits, the ability to fly puts certain physiological and ecological restrictions on birds, including restraints on possible feather morphologies (especially remiges and rectrices). In response, when ecologically favorable, many separate lineages of birds have evolved flightlessness, either completely or during a fixed time in their annual cycle. Flightless birds can generally be separated into three categories: (1) wing-propelled divers that do not fly but use relevant structures for flight to “fly” underwater, (2) entirely flightless, non-wing-propelled divers, and (3) species that lose and regain flight during their annual cycle. Wing-propelled divers that do not fly but use relevant structures for flight to “fly” underwater includes all the penguins and a number of extinct birds in the alcid family, including the recently extinct Great Auk (*Pinguinus impennis*). These taxa retain many of their structural adaptations for flight despite their flightless state because they use them for swimming. However, their feathers are an exception - the release of constraints associated with flight have allowed their feathers to evolve very specific morphologies associated with strong swimming selective pressures (Kulp et al. 2018). Entirely flightless, non-wing-propelled divers include all flightless birds that do not use their wings for any function approximating flight. This includes the ratites, which have lost flight convergently multiple times (Harshman et al. 2008), as well as foot-propelled flightless diving birds, such as the Pleistocene anatids in the genus *Chendytes* (Livezey 1993), and extant flightless ducks (Anatidae), grebes (Podicipedidae), and rails (Rallidae). These taxa tend to lose structural and physiological adaptations for flight - the keel and wings tend to become reduced over time, and feathers, especially those previously constrained due to flight, increase morphological diversity (Livezey 1988, 1989). Species that lose and then regain flight during their annual cycle include taxa that undergo a simultaneous molt of the wing feathers, which induces a flightless period during molt. Birds that use this strategy include ducks (Anatidae), geese (Anseridae), grebes (Podicipediae), rails (Rallidae), and loons (Gaviidae). These birds can forage for food and escape predators without flying and thus condense the molting period by undergoing a flightless period during simultaneous wing molt.

Feathers show many adaptations for different types of flight. Generally, birds that need to fly farther and faster have longer, narrower wings, which trade reduced maneuverability and flight initiation ability for increased efficiency (Lockwood et al. 1998). Birds that fly in short bursts tend to have rounded wings, which are less efficient, but require less energy for take-off, and are more maneuverable (Tobalske et al. 2003). Soaring birds, (e.g. some raptors (Accipitriformes), pelicans (Pelecanidae), and storks (Ciconiidae)), have evolved notched or emarginated outer primaries, which allows air flow around each of the outer primaries. This serves to slow the flight momentum, so that the birds can turn in tight circles and make more efficient use of thermal updrafts during soaring flight (Cone 1962).

Aerial Maneuverability

In addition to the maneuvering capabilities provided by lift generated by the wings and tails of flighted birds, some species of birds have elongated tails that aid in aerial maneuvering (Figure 3e). These elongated rectrices increase aerial maneuverability for pursuit of agile, volant prey. Species with rectrices associated with aerial maneuverability tend to show elongated (e.g. *Accipiter*) or forked tails with outer rectrices noticeably longer than the inner rectrices, *e.g.* frigatebirds (Fregatidae) and several swallows (Hirundinidae), especially the genus *Hirundo,* as well as the kite genera *Elanoides* and *Chelictinia,* and some terns (Laridae) and swifts, notably the palm-swifts (*Cypsiurus* and *Tachornis*). Terns do not forage for aerial prey, but do use sharp turns in flight to dive on fish with precision. The elongated outer tail feathers of species with forked tails function by disrupting the lift generated by the tail when angled down, thus causing rapid changes in the direction of flight of the bird (Norberg 1994), and enabling sharp turns.

Birds' tails produce lift in flight (Pittman et al. 2013), but the outer tail feathers of species with deeply forked tails cannot produce lift past the length of the short inner rectrices (Tubaro 2003). Thus, elongated outer tail feathers only produce lift along the base of the feather, then serve to disrupt lift when angled downward for abrupt aerial maneuvering along the length of the feather past the tip of the shortest rectrix. In some species with very long, forked tails, *e.g.* nightjars (Caprimulgida*e*) in the genus *Uropsalis*, flycatchers (Tyrannidae) such as Fork-tailed Flycatcher (*Tyrannus savana*) and Scissor-tailed Flycatcher (*T. forficatus*), and many hummingbirds such as the genera *Lesbia, Eupetomena*, and *Sappho*, the outer rectrices have become extremely elongated, presumably under sexual selection (see *social display* -- *sexual display*). These long, forked tails may have first evolved for increased aerial foraging ability and become exaggerated over time due to sexual selection. Birds with long, forked tails show a reduced stiffening of rectrices in the outer tail feathers, concordant with a release in ability to produce lift past the length of the shortest rectrices, and a decrease in need to support birds' weight in the air (Tubaro 2003).

Swimming

All wing-propelled divers use feathers in swimming. These include the auks, penguins, some waterfowl, and some tubenoses (Procellariiformes), most notably the diving-petrels (*Pelecanoides*), which forage primarily by swimming underwater. These birds show various morphological adaptations in their feathers, which generally reflect tradeoffs between use of the wings for swimming vs. flying. Diving birds that also spend much of their lives in flight tend to have long, thin primaries and secondaries (Spear and Ainley 1997). Birds such as shearwaters that spend much of their life on the wing but do swim underwater when chasing prey, fall into this category. Intermediate groups, such as auks and diving-petrels, which spend comparatively less time in flight, have shorter wings and relatively smaller feathers. Penguins are completely flightless but rely on their wings to "fly" underwater, and show extremely shortened, flattened flight feathers with a very stiff rachis and lengthened calamus (Stettenheim 1976), and flattened rami (Kulp et al. 2018), which streamlines and strengthens the trailing edge of the wing, as well as trapping air between the feathers and skin for underwater thermoregulation. Kulp et al. (2018) found that penguin feathers have reduced the size of air-filled vacuole in feather barbs and also have evolved unusual keratin nanofibers in the barbs. These keratin nanofibers produce blue structural color in some feathers, but Kulp et al. (2018) hypothesized that they arose for hydrodynamic or other structural functions and not signaling.

Buoyancy

Many birds waterproof their feathers through structural modifications (see *Waterproofing*). A side effect of the waterproofing of feathers is the buoyancy afforded by an increased area of impermeable surface. This buoyancy allows birds to float on top of the water in a way no other tetrapods can (Figure 3k). Buoyancy has allowed many groups of birds, notably most waterfowl (Anseriformes; Stephenson 1993), alcids (Alcidae), loons (Gaviiformes), and grebes (Podicipediformes), to live most of their lives floating on water, but can also be detrimental to birds that need to feed underwater (Hustler 1992). Because of the disadvantage for birds that need to forage underwater, birds have several ways of adjusting their buoyancy over evolutionary time. Birds can increase buoyancy through increased retention of air in their feathers (Lovvorn and Jones 1991) or decrease their buoyancy by increasing their overall body density, especially in their bones (e.g., cormorants (Phalacrocoracidae) and penguins (Sphenisciformes; Lovvorn and Jones 1991)), or by increasing water permeability in feathers (e.g. in cormorants; Grémillet et al. 2005, Wilson and Wilson 1997). Despite the disadvantages buoyancy poses for diving ability in some species, others can use buoyancy as an advantage. In penguins, buoyancy can assist a deeper dive by providing a passive ascent from deep foraging bouts (Sato et al. 2002).

Balance/Bracing

Several groups of birds use their rectrices to brace themselves against a vertical substrate (Figure 3c). Rectrices generally are adapted to bear weight in flight, with a stiffened rachis compared to body feathers and articulation to the pygostyle (Pittman et al. 2013). These load-bearing functions may have provided a preadaptation for the use of rectrices for balance or bracing. Several unrelated groups that climb trees, such as woodpeckers (Picidae; Bock 1999), woodcreepers (Furnariinae; Fjeldså et al. 2005), and treecreepers (Certhiidae; Norberg 1986) or cliffs (Wallcreeper; *Tichodroma muraria*) use their rectrices to brace their body against the vertical surface (Norberg 1981). The oxpeckers (Buphagidae), which cling vertically to large mammals, also have stiffened rectrices for support (Plantan 2009). Tails used as a brace have stiffened rectrices characterized by noticeably wider rachises (Tubaro 2002), as well as rachises that extend past the feather vane, resulting in tail spines. These birds also use their rectrices to brace for applying pressure to the surface, such as drilling in woodpeckers (Liu et al. 2015). This adaptation opens a novel niche for birds in the form of foraging on vertical surfaces, which may create ecological opportunity – although Claramunt et al. (2012) found no increase in speciation rate after the evolution of stiffened rectrices in the Furnariidae. This adaptation can also be useful for birds that sleep while clinging to a vertical surface (e.g., leaftossers (*Sclerurus;* Van Els and Whitney 2011)). Some swifts (Apodidae), especially those in the genera *Chaetura* and *Hirundapus* cling vertically to hard substrates and have similar tail spines. Hummingbirds in the genus *Oreotrochilus* also show this same adaptation and behavior (Carpenter 1976). Other species that only occasionally use their tail for balance and support also show stiffened rectrices with rachises that extend past the feather vane, such as ovenbirds in the genera *Leptasthenura* (Engilis and Kelt 2011), *Synallaxis*, and *Cranioleuca* (Feduccia 1973). These species tend to forage acrobatically, using their tails to brace themselves and balance when foraging upside down or briefly against vertical surfaces. The earliest known fossil of a treecreeper (Certhiidae) shows structural adaptations for vertical climbing, indicating that climbing originated in that lineage by at least the early Miocene (Manegold 2008). The furnariid woodcreepers also date molecularly to the early Miocene, but are not represented by any fossils older than the Pleistocene for comparison. (Derryberry et al. 2011).

The evolutionary history of rectrices that are stiffened for balance may have been guided by general forest type change during the Oligocene-Miocene transition. Woodpeckers are represented by one fossil from the Oligocene (Mayr 2001), but the morphology of that fossil was intermediate between trunk-climbing and non-climbing Piciformes, and so it is difficult to assign a date to the origin of climbing in woodpeckers. Molecular dating (Prum et al. 2015, Shakya et al. 2017) suggests a divergence of the non-climbing Wryneck (*Jynx torquilla*) from other woodpeckers during the early Miocene or Oligocene-Miocene transition, but not enough data exists to determine when vertical climbing evolved relative to this divergence. That multiple lineages appear to have independently evolved vertical foraging on trees during or close to the early Miocene may potentially be attributed to the expansion of temperate deciduous forest during the Oligocene-Miocene transition (Jiménez-Moreno 2006).

Physiology

Thermoregulation

Feathers allow birds to maintain homeothermy and may have been integral to the evolution of their endothermy (Grigg et al 2004, Ruben 1995). Offering a glimpse into the importance of feathers for thermoregulation, altricial birds that are born without feathers experience a brief period of poikilothermy before their first molt brings them the thermoregulatory capabilities of feathers (Breitenbach and Baskett 1967, Gotie and Knoll 1973). These thermoregulatory abilities have allowed birds to colonize some of the harshest environments on earth (D'alba et al. 2017). Insulation against cold allows birds to forage in Arctic waters and snow in the winter (Grémillet et al. 2001, Veghte and Herreid 1965) and escape body size limits in cold environments that non-feathered animals experience. For example, very small birds are able to overwinter in extremely cold climates without hibernating (Dawson et al. 1983, Hill et al. 1980, Steen 1958, Swanson and Liknes 2006) by decreasing the minimal body weight required for homeostasis via endogenous thermogenesis (Veghte and Herreid 1965). In general, birds living in cold environments have longer down feathers with lower barb and barbule densities, to trap more air (Pap et al. 2017), or a greater plumulaceous portion of the feather (Barve et al., 2021). Variation in feather barbs and barbules in pennaceous portions of the feather has implications for reflectance of near infrared light, suggesting that microstructure may broadly be involved more broadly in thermoregulation (Igic et al., 2018, Stuart-Fox et al., 2018) Feathers also play a thermoregulatory role in hot environments. An underappreciated role of feathers in thermoregulation is in deflection of solar radiation to keep birds cool (Medina et al. 2018). For example, unlike kangaroos who must seek shade during the hottest parts of the day, in the harsh Australian desert, emus do not need to seek shade, because feathers are superior to fur at reflecting solar radiation (Dawson and Maloney 2004).

One reason feathers function so well for thermoregulation is that they provide a thermal buffer between birds and their environment, and birds can behaviorally modify this buffer (Wolf and Walsberg 2000). Birds can manipulate their thermoregulatory properties through position, by erecting feathers to increase their total volume and make them warmer (McFarland and Budgell 1970), or by moving feathers to expose apteria, where heat can be transferred to the surrounding air to make them cooler (Gerken et al. 2006). Feathers insulate against cold by trapping air (Dove and Agreda 2007, Stettenheim 2000), which when underwater can increase the buoyancy of diving birds (see *buoyancy* and *waterproofing*). However, even birds with feathers that allow partial water permeability to decrease buoyancy, still trap a small air layer near their body, which continues to act as an efficient insulator, even in very cold water (e.g., cormorants (Grémillet et al 2005)).

Protection from solar radiation

Feathers provide protection to both their bodies and other feathers against solar radiation. At least one author has proposed that body protection from solar radiation as the original function of early feathers (Regal 1975). When feathers are not present or insufficient to protect from solar radiation (white feathers) in environments with high ultraviolet irradiation birds tend to have black skin (Nicolaï et al. 2020). Solar radiation is probably a primary driver of feather degradation (Lennox and Rowlands 1969, Surmacki 2008), and degraded feathers quickly lose their aerodynamic function (Merilä and Hemborg 2000). Feathers fade through the year from solar radiation (Hasegawa et al. 2008). The wings and tails of birds are folded in a way such that the outer feathers stack under both the inner feathers and coverts (Figure 3o). The effects of this shading is visible in older feathers that have significant exposure to the sun, with a darker, stronger feather vane where the feather is covered, that contrasts markedly with a noticeable worn and lighter colored feather tip where exposed on the folded wing (Figure 3b). The outer primaries, which contribute most to flight, are entirely or almost entirely hidden under other feathers when a bird's wing is closed. Even in birds with high aspect ratio wings that show a long primary extension past the secondaries and tertials, each individual primary feather is almost entirely covered by feathers above it when the wing is closed. The role of feather protection in the evolution of the shape of birds' wings has not been studied, and it may be that an interplay between protection of the most essential feathers for flight and aerodynamic optimization has contributed to the evolution of modern bird wing shapes. Research into the role of feather protection in the evolution of wing shape could potentially test the aerodynamics of wings with shorter or absent tertials or coverts to examine whether current wing shapes are idealized for flying, or are influenced by the need for feather protection. Further, the shapes of wing coverts in early birds such as *Anchiornis huxleyi* and *Archaeopteryx lithographica* were morphologically distinct from modern birds (Longrich et al. 2012), opening the possibility for the separate roles of flight dynamics and feather protection combining to drive early wing shape evolution in birds.

Waterproofing

Waterproofing of feathers aids in thermoregulation, buoyancy, and maintaining feather structural integrity and a low weight for flight in birds, allowing use of aquatic, marine, and cold environments. The waterproofing of feathers had previously had been assumed to be a product of the oily secretions that birds rub on their feathers from the uropygial gland, but multiple studies have demonstrated that uropygial oil does not provide waterproofing for feathers (Rijke 1968, Rijke and Jesser 2011, Giraudeau et al. 2010). Uropygial oil appears to aid waterproofing only through the maintenance of feather microstructure by decreasing the rate of physical wear on the feather (Giraudeau et al. 2010). Waterproofing in feathers is instead a product of feather microstructure through capillary-related physical phenomena (Figure 3a). Feather barbules with large angles form air pockets that are impenetrable by water droplets (Bormashenko et al 2007, Liu et al. 2008, Rijke et al. 2000). Some diving birds allow partial plumage wettability in order to decrease their buoyancy (see *buoyancy*) through structural modification of the distal half of body feathers. The pennacous section of feathers appears unmodified and traps air for insulation, but the plumaceous section of the body feathers are looser, and do not trap air (Grémillet et al. 2004, Rijke et al 1968). Water surface tension is key to the phenomenon of waterproofing in feathers, because the physical mechanism of waterproofing relies on droplet formation (Stephenson and Andrews 1997). Oils reduce the surface tension of water, and so when birds encounter oil in their environment, their waterproofing can be seriously compromised (Whitmer et al 2018). When oiled, droplets fail to form on top of the feather, which inhibits both thermoregulation and buoyancy. Oil spills in marine environments, such as the *Exxon Valdez* and *Deepwater Horizon* disasters thus can cause mass mortality events in birds (Irons et al. 2000, Piatt et al 1990, Haney et al. 2014) by compromising the ability of birds' feathers to repel water, in addition to the detrimental health impacts of direct chemical poisoning.

Protection from parasites

Feathers protect birds from parasites by forming a physical barrier over the skin, or by hosting and/or producing chemical deterrents. Birds are plagued by a variety of parasites, including mosquitoes, ticks, mites, hippoboscid flies, and feather-degrading bacteria (see *Chemical Defense*). Feathers provide a physical barrier that mosquitos cannot get through, and so most mosquito bites on birds are on the legs and exposed skin on the face (Webber and Edman 1972). Some species of birds appear to rely mostly on movement and position of the head and feet to deter mosquitos (Darbro and Harrington 2007), but Darwin's finches (*Geospiza*) have been known to rub the leaves of the tree *Psidium galapageium* on their feathers, which appears to act as a chemical repellent to mosquitoes and to inhibit growth of larvae (Cimadom et al 2016). Additionally,feathers may give off compounds that deter some species of mosquitoes such as isobutyl butyrate, naphthalene, hexadecane, and *trans*-limonene oxide (Jaleta et al. 2016). The mechanism by which these compounds are produced and their evolutionary origins in the host-parasite arms race, is unknown. However, the diversity of volatile oils in the preen oils of birds (Whittaker et al. 2010) suggests the uropygial gland may be the source.

In addition to protecting themselves, birds also must protect their feathers against feather-degrading bacteria, and they primarily do so through chemical defenses and the internal feather pigments that produce color. For example, the Hoopoe (*Upupa epops*), uses the external application of a uropygial gland oil containing antibiotic compounds for defense against keratinolytic bacteria, which is produced by symbiotic bacteria living in their uropygial glands (Ruiz-Rodríguez et al. 2009, Soler et al. 2008). Feather bacteria can be detrimental to the condition of feathers (Atalo and Gashe 1993, Riffel and Brandelli 2006), and this antibiotic mutualism may exist in other species (Shawkey et al. 2003). The diversity and distributions of these bacterial mutualisms may provide a fruitful avenue for research into defenses against ectoparasites, which may be harmful to feathers (Barbosa et al. 2002). In addition to antibiotic compounds, feathers may also be a substrate for defense against ectoparasites by extruding or containing odor-emitting compounds (Clayton et al. 2010), but the functions of feather odors remain poorly studied (see *Odor*).

In addition to oily coverings discussed above, some feather pigments appear to provide resistance against feather-degrading bacteria (Grande et al. 2004), especially the widespread dark melanin pigments (Burtt and Ichida 2004, Goldstein et al. 2004, Gunderson et al 2008). The efficacy of melanin in resistance to degradation by bacteria may play a role in Gloger's rule (Burtt et al. 2004), where darker plumage occurs in humid environments (Delhey 2019). The incorporation of melanin into plumage may act to broaden the environmental niches that individual species can inhabit through local adaptation to bacterial loads via feather pigment deposition. Unlike the other brightly colored carotenoid pigments, psittacofulvins, pigments specific to parrots (Psittacidae) are as effective as melanin at protecting against bacterial degradation (Burtt et al. 2010), which may relate to the radiation of parrots in humid tropical zones. Research into the role of psittacofulvins in the feather of parrots to parrot diversity should investigate whether parrots follow Gloger's rule, and where on the tree of life psittacofulvins may have evolved, relative to potential rate changes in diversification in parrots.

Nest lining

Birds use their own feathers and feathers from other birds (Winkler 1993) to line their nests. In the Fork-tailed Palm-Swift (*Tachornis squamata*), individuals even attack and forcibly remove feathers from other birds in flight (Whitney 2007). This lining acts as extra insulation for the incubation of eggs and thermoregulation of chicks in the nest (Møller 1984). Birds can adjust nest thermoregulation by adding or removing feathers according to ambient temperature (Liljesthröm et al. 2009). In addition to thermoregulation, some evidence suggests that feathers used to line nests may also reduce the bacterial load of the nest (Peralta-Sanchez et al. 2010), and the soft nest lining that muffles sounds may contribute to reducing detection by predators (Møller 1987). Some studies have found that feathers reduce the ectoparasite load in nests (Winkler 1993), but other experiments have found no effect on ectoparasite load (Lombardo et al. 1995, Stephenson et al. 2009), and at least one study found an increase in the number of blowflies in nests with an increased number of feathers in the lining (Dawson et al. 2011). Nest lining with feathers is widespread among species (Hansell 2000) but is most well-known in the swallows (Hirundinidae). In swallows, at least one study found that nests with feathers experimentally removed produced chicks with lower body mass and longer incubation times compared to control groups (Møller 1991).

External sensation (non-foraging)

Filoplumes are long thin feathers with elongated rachi and reduced vanes, and are generally enervated at the base. Intermixed throughout bird plumage, they tend to extend beyond the contour feather, especially on the back of the head and nape of a bird. They may act to sense when contour feathers are out of place (Necker 1985), especially in body regions not visible to the bird (e.g., the nape (Clark and Cruz 1989)). In addition to contour feathers, primary flight feathers are also associated with filoplumes, and each filoplume shows a distinct morphology to its associated primary; suggesting a role for the filoplumes in sensing relative position of each flight feather (Rohwer et al. 2021).

Feeding

Foraging

Feathers directly aid birds in foraging for prey by protecting the eyes and nares, acting as whisker-like tactile sensors, and acting to flush prey from refugia. Rictal bristles are stiffened feathers that lie in front of the eye and along the edge of the mouth (Figure 3g). The function of these rictal bristles has been debated, with some authors suggesting that they function as a funnel to guide prey towards the mouth (Lederer 1972). However, experiments show that the removal of rictal bristles does not affect foraging (Conover and Miller 1980), and so prey funneling seems unlikely. Other authors have suggested tactile function for these rictal bristles (Cunningham et al. 2011). Herbst corpuscles, nerve endings that detect tactile sensations, are attached to the rictal bristles, are present across deeply related groups of birds (Cunningham et al. 2011). This suggests at least a partly tactile function for birds. A notable example is the nocturnal kiwi family (Apterygidae) in which rictal bristles appear to have converged morphologically and functionally upon mammalian whiskers. Rictal bristles are noticeably present in many insectivorous birds, especially those that eat large prey relative to their body size, but most diurnal foraging insectivores would have little need for tactile function in rictal bristles. Thus, current thinking is that these bristles act primarily to protect the eyes from sharp arthropod legs during prey capture and manipulation (Conover and Miller 1980), but no data conclusively demonstrate this function. Many birds have feathers that cover the nearest portion of the nares and are hypothesized to serve as physical or thermal protection (Wunder and Trebella 1976), although the functions of nares-covering feathers has not received widespread study. One example of feathers as nares protection during foraging is the tightly packed feathers that protect the nares of honey-buzzards (*Pernis*) from the bees they eat (Stettenheim 1976).

Birds sometimes use their feathers directly in foraging to attract or flush prey. For example, the Black Heron (*Egretta ardesiaca*), periodically uses the wings to create shade that attracts prey. Alternatively, many species of insectivores have hidden white spots in the wings or tail that they expose regularly and abruptly during foraging. This method of “flush-pursuit” foraging has been documented to increase foraging efficiency in several New World wood-warblers (Parulidae): the Painted Redstart (*Myioborus pictus;* Jablonski 2001), Slate-throated Redstart (*M. miniatus;* Mumme et al. 2006), American Redstart (*Setophaga ruticilla;* Robinson and Holmes 1982), and Hooded Warbler (*Setophaga* citrina; Mumme 2014).

This foraging method is likely much more widespread, given the diversity of insectivorous birds that actively flash white in their wings or tail during foraging (Randler 2016).

Sound reflection

Some birds rely on their hearing to locate prey, and feathers can reflect sound in a way that amplifies and localizes sounds to improve directional hearing. This is best known in the barn owls (Tytonidae), which have a facial disc of feathers that amplifies and localizes sounds at the ears (Coles and Guppy 1988, Hausmann et al. 2009) to help locate prey in total darkness. An unrelated genus of diurnal hawks, the harriers (*Circus*), also has a similar facial disk, and show a superior ability to locate prey by sound when compared to other diurnal raptors (Rice 1980). Like many owls, harriers also have velvety feathers that reduce sound during flight (see *Crypsis*).

Stomach protection and digestion

Some species of birds are known to ingest feathers. After ingestion, grebes (Podicipedidae) form a pellet, almost entirely composed of their own molted feathers (Piersma and Van Eerden 1989), had been thought to surround bones and other sharp objects (Simmons 1956), and may protect their stomachs from puncture. However, Jehl (2017) argued that feathers instead retain food in the stomach for chemical digestion and filter undigested food from entering the intestine. Feather eating is also known in captive birds, especially parrots and chickens (McKeegan and Savory 1999), but appears to be a nonfunctional behavioral disorder. This behavior in fact may be detrimental to nutrition absorption because chickens that ingest more feathers pass food more quickly through their digestive tracts (Harlander-Matauschek et al. 2006).

Water Transport

Sandgrouse (Pteroclidae) often live in arid regions and nest far away from water sources (Benitez-Lopez et al 2014). The males in this family transport water to their precocial nestlings by carrying water in their feathers from a water source back to the nest, a behavior that they exhibit even in captivity with ample access to water (Cad and Maclean 1967). To transport water, adult sandgrouse saturate specialized feathers on their underparts (e.g., belly) with water. These feathers show helically coiled barbules with concave transverse sections (Joubert and Maclean 1973). These barbules lack hooklets, and when wetted, the coiled barbules unfurl resulting in an increase in their surface area (MacLean 1983) and hold water through capillary force, and perhaps via direct interaction with the structure of the barbule keratin (Rijke 1972). Water transport is relatively rare in the animal world (Ishii et al. 2013), and so this adaptation to life in arid areas using the evolution of feather structure highlights the functional adaptability of feathers for birds.

Communication

Mate Choice

Sexual selection pertains to selection on an organism’s phenotype through mate choice or intraspecific (e.g. territorial) competition (see *Social Selection*). In birds, a large part of the visible phenotype available as display for mate choice or competition is presented by the feathers, and thus in many species of birds feathers have evolved in response to sexual selection (Figure 3h). The role of sexual selection on bird plumage has received much study and will only be touched on briefly here (Hill and McGraw 2006). Many of the famous colors and shapes of feathers that have captivated people’s imaginations for centuries are involved in sexual display, and elaborate ornamentation in feathers inspired Darwin’s original formulation of the idea of sexual selection (Kirkpatrick et al. 1990). Darwin realized that elaborate plumages such as the peacock’s tail could not be explained by natural selection alone, writing to a friend "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick" (Darwin Correspondence Project 2020). One way feathers can be shaped by sexual selection is when some aspect of the feather is an honest signal of individual quality, for example through a coloration mechanism that must reflect a high-quality diet or metabolic requirements, such as carotenoid pigments (Hill and Montgomerie 1994, Koch et al. 2019, Piersma and Jukema 1993, Weaver et al. 2018). Another potential way that plumages can convey an honest signal of quality is through a “handicap”, (i.e., a plumage that makes a bird more visible to predators). Fisher (1930) proposed that when females prefer a showy trait, that trait can be selected for by female preference alone, and may end up in “runaway” selection, in which a trait is exaggerated to a high degree, for example in the tail of a peacock. However, some recent research has found that female preference may be variable and at least partly driven by factors extrinsic to males’ plumage (Chaine and Lyon 2008), and may in fact be purely driven by intrinsic arbitrary aesthetic preferences of each species (Prum 2012). Feathers are generally involved in sexual display through their shape or coloration, although in rare cases through odor or sound generation (both covered here in their own sections). In general, sexual traits in birds tend to be more exaggerated in species with high variance in reproductive success, such as polygynous and promiscuous species, and especially lekking species. Perhaps the most extreme and well-known example of sexual display in feathers is among the birds of paradise

(Paradisaeidae), the males of which exhibit extraordinary feather colors and shapes for use in sexual display (Scholes 2008). These feathers can be integrated into complex behaviors, and in birds of paradise, visual feather ornamentation is positively correlated with behavioral display complexity (Ligon et al. 2018).

Sexual display in feathers is generally manifested through conspicuous coloration or the elongation or exaggerated shape of a feather. Rectrices are not often conspicuously colored, but some birds do show conspicuous colors in their rectrices, especially when elongated. In some species, such as the Red-tailed Comet (*Sappho sparganurus*) and the peacocks, the majority of conspicuously colorful plumage is on the tail. Feather elongation for display tends to occur in the rectrices, the wing coverts, or tail coverts, although some birds elongate other feathers, such as the spectacularly modified second primary of the Pennant-winged (*Caprimulgus vexillarus*) and Standard-winged nightjars (*Caprimulgus longipennis*) (Fry 1969). Conspicuous coloration can be produced by a number of different coloration mechanisms. Recent research has found sexual dichromatism in birds that is cryptic to the human eye because of differences between human and avian visual systems, including the ability to perceive ultraviolet reflectance (Andersson et al. 1998, Burns and Shultz 2012, Eaton 2005, Mullen and Pohland 2008, Shawkey et al. 2005). In one extreme circumstance, ephemeral pink coloration caused by the fluorescence of porphyrin pigments can wear off as quickly as 10-15 minutes in Bustards, and has been hypothesized to signal the first sexual display of an individual male in a given season (Galván et al 2016).

Social Selection

Individuals within a species can compete for access to mates, or access to resources (e.g. territories), generally termed social selection (Tobias et al. 2012). Male birds often compete with one another for access to females and territories. Similar to their importance in mate choice, in many species of birds, feathers can signal status among individuals to avoid potentially dangerous physical confrontations. These status signals can be in the form of color contrast or brilliance, or the size of a plumage color patch (Figure 3m). Males with larger or more enhanced plumage signals tend to win fights (Hagelin 2002), and, in at least the red junglefowl (*Gallus gallus*), enhanced plumage signals are tightly associated with blood testosterone level (Ligon et al. 1990). In the Harris's Sparrow (*Zonotrichia querula*), the size of the black bib patch on males indicates an individual male's social status. Experimental manipulation of the bib patch size in Harris's sparrows leads to active persecution by other males (Rohwer and Rohwer 1978), indicating that males monitor the congruence between the feather signal and an individual's behavior. The line between traits for male–male competition and for female choice is fuzzy, however, because male–male competition often facilitates female access, and females tend to choose males with the same traits involved in male–male competition (Griggio et al. 2007). Most research on intraspecific competition has focused on male-male competition, but competition also can exist among females, particularly for resource access (Rosvall 2011). Recent work has shown evidence that plumage ornaments can also be correlated with individual quality in females (e.g. white feather moustaches in Inca Terns (*Larosterna inca*), Velando et al. 2001). Diamant et al. (2021) identified that more than 25% of hummingbird species had females that resemble male-like coloration, and female-limited polymorphism is associated with ecology, migratory status, and social dominance. Future studies should consider both sexes when investigating correlations between plumage ornaments and social interactions.

In addition to competition, plumage ornamentation appears to play a role in parental choice; where colorful plumages appear to confer advantages to chicks when being cared for, such that more ornamented chicks are preferentially fed by the parents (Figure 3p; Lyon et al 1994). In this case, parents are directly selecting for chick plumage through differential investment in care, based upon plumage color. More work is needed to understand why juvenile birds develop ornamented colors in the first place; however, recognition of brood parasites does not appear to play a role (Lyon and Shizuka 2020).

While some young birds are ornamented, others are duller than adults. The phenomenon of birds taking multiple annual cycles to reach a definitive plumage is known as delayed plumage maturation. The origin and evolutionary causes of delayed plumage maturation have been debated in the literature (see *molt: change of function*); but the pattern is broadly displayed across birds, especially highly social birds and birds with leks, in which delayed investment in breeding may result in higher social status in future breeding seasons (Hawkins et al 2011).

Secondary Visual Display

Many species of birds use their feathers for visual display, but some species use other species' feathers for a secondary visual display. Male bowerbirds (Ptilonorhynchidae) build decorative structures called bowers as part of their courtship display (Gilliard 1956). In at least the Satin Bowerbird, this display can include the feathers of other birds (Frith and Frith 2019). Satin Bowerbirds prefer to decorate their bowers with blue objects (Borgia 1985), but do not grow blue feathers. Instead, they procure blue feathers from other species, at least some of which are primary feathers from Crimson Rosellas. (Frith and Frith 2019). These feathers appear to be a limited resource, as male Satin Bowerbirds commonly steal blue feathers out of each other's bowers (Borgia and Gore 1986). Because these feathers are detached from the bird (and are often from other individuals), this visual display can be considered a secondary use of the feather for visual courtship display to females.

Sound generation

The importance of feathers as a mechanism for sound generation has not been fully appreciated until recently. At least five families of birds, hummingbirds (Trochilidae; Figure 3i), manakins (Pipridae), shorebirds (Charadriiformes, notable the Snipe *Gallinago spp.* (Reddig 1978), Nightjars (Caprimulgidae), and New World Flycatchers (Tyrannidae), use their feathers to generate sound during sexual displays. Other species birds, notably pigeons and doves (Columbidae), use noise generated by their feathers to startle predators and allow time for escape (Coleman 2008). Most birds' flight feathers appear to be capable of producing some sort of sound via aeroelastic flutter, and so the use of feathers to make sounds by unrelated species may be due to an intrinsic quality of feathers, manifested convergently in different groups (Clark and Prum 2015), such as snipe (*Gallinago*; Reddig 1978). Aeroelastic flutter appears to be the mechanism for sound production in hummingbird feather noises during sexual display (Clark et al. 2011, Clark et al. 2013). Feathers that do produce sounds often to show abnormal shapes, though these modifications can be hard to detect (Clark et al. 2016). These shapes are likely to facilitate noise production, including in the wings (Clark 2008) and tails (Clark and Feo 2008) of hummingbirds, and in the wings of pigeons (Niese and Tobalske 2016) and Fork-tailed Flycatchers (Gómez-Bahamón et al., 2020). Aeroelastic fluttering cannot explain all feather sounds in birds however, some groups of birds produce sound with feathers that appears to not involve aeroelastic flutter through wing clapping or fluttering. One of these stands out in particular: the manakins (Pipridae). Manakins are an excellent example of feather sound production using an alternative mechanism. They produce sound through physical interactions among feathers, which can be slightly to highly modified for sound production across species (Prum 1998, Bostwick 2000), and have evolved a variety of mechanical feather sounds for use in their sexual displays.

Social Mimicry

The plumages of some birds appear to have evolved to mimic other species (Figure 3n). The extent of this phenomenon remains difficult to ascertain due to potential for convergent evolution for ecological reasons, but some have suggested that social mimicry may be widespread (Prum 2014, Prum and Samuelson 2016). Social mimicry is hypothesized to protect a smaller species from attack by a larger, more socially dominant species (Prum 2014). One example is the Zone-tailed Hawk (*Buteo albonotatus*), which appears to mimic Turkey Vultures in order to prevent alarm in potential prey (Willis 1963, Mueller 1972, Zimmerman 1976). Woodpeckers (Picidae) are the best-studied system of social mimicry in birds. Prum (2014) suggested that at least two species of woodpeckers have evolved convergent plumage for social mimicry. Miller et al (2019) examined the evolution of plumage from a viewpoint of mimicry across the family, and found that despite ecological pressures on plumage, many woodpeckers are most similar in areas of geographic overlap. The authors interpret this finding as evidence for fairly extensive interspecific social mimicry throughout the global distribution of this family. The toucans (Ramphastidae) and flycatchers (Tyrannidae) are other widespread groups with apparent mimicry in plumage, for which larger and smaller toucans evolved similar plumage in sympatry, and flycatchers independently evolved yellow underparts and black-and-white striped heads many times in species in sympatry with the Great Kiskadee (Prum and Samuelson 2016).

Batesian Mimicry

Toxins are scarce in birds, so the recent discovery of Batesian mimicry in birds is surprising. The juvenile plumages of most birds are cryptic, likely to aid predator avoidance in young birds that cannot yet outfly or outrun predators. However, some juvenile cotinga plumage patterns (Cotingidae) in the genera *Laniocera* and *Laniisoma* are conspicuously bright and strongly patterned (Figure 3d). The current hypothesis is that these unusual plumage patterns use Batesian mimicry on toxic caterpillars living in their environments (D'Horta et al. 2012) to trick predators into thinking these juvenile birds are toxic caterpillars. Although this hypothesis has not been directly tested, it is supported by the addition of behavioral mimicry of caterpillar movements in the nest (Londoño et al. 2014). Pitohuis in New Guinea have also been proposed to exhibit Batesian or Mullerian mimicry (see *Chemical Defense*).

Crypsis

Baker and Parker (1979) suggested that the primary function of feather coloration may be evasion of detection by blending in with the environment, or crypsis (Figure 3f). Crypsis can be advantageous by allowing individuals to avoid detection by both predators and prey. Feather patterns can contribute to crypsis either through background matching (Merilaita and Lind 2005) or outline disruption (Thayer and Thayer 1909). Background matching occurs in many species of birds through complicated feather patterns that blend in with leaves or bark, especially nocturnal birds (such as owls (Strigiformes) and nightjars (Caprimulgidae)) that remain motionless through the day. The ability to blend in with an individual's surroundings directly impacts fitness in these species (Troscianko et al. 2016). They will tend to sit still rather than attempt to flee when a predator is nearby, especially when on the nest, relying on their camouflage for protection (Wilson-Aggarwal et al. 2016). In diurnal species, background matching can occur through countershading (Götmark 1987, Rowland et al. 2007) or complex patterns that may match rocks or grassy habitats. Tanagers have been shown to have more complex, colorful plumage patterns in closed than open environments, which also could be related to background matching (Shultz and Burns 2017). Many species of tropical birds with green plumages fall into this category, and many a field ornithologist has been surprised by the way seemingly flashy parrots can disappear into the leafy canopy of a tree.

Birds can alter their plumage patterns throughout the year through molt. Environments vary throughout the year, and many species of birds take advantage of molts to alter their plumage to match that variation and maintain crypsis. The most famous example of this is in the ptarmigans (*Lagopus*; Phasianidae), which cycle through brown, white, and patchy plumages through the year to blend in with the variable snow cover inherent in their seasonal environments (Hohn and Braun 1980, Jacobsen et al 1983, Pyle 2007).

In addition to visual crypsis, some species specifically silence the sounds their feathers make (Klän et al. 2010, Chen et al. 2012). In addition to visual crypsis, owl wings are adapted to reduce flight noise. This may be to mask noise from prey or for self-masking, to improve hearing in flight for owls (Clark et al. 2020). Either of these functions could possibly be considered a form of crypsis. This silent flight is achieved by the velvet and fringe textures of wing feathers in owls and other raptors (Clark et al 2020).

Distraction Display

Deliberate display to predators is most pronounced in shorebirds (Charadriiformes; Gochfeld 1984, Armstrong 1954). Birds that engage in distraction display often feign injury by dragging a wing, and feathers are explicitly involved in this display at least in the Killdeer

(*Charadrius vociferus*), which show a patch of conspicuous red plumage on the rump during their distraction display. In addition, Royal Flycatchers (*Onychorhynchus spp.)* perform an elaborate feather display when captured (Figure 3j; Chaves 2006), which has been hypothesized to perhaps function to distract predators (Graves 1990)

Odor

Some feathers give off distinctive smells. The only example of feather odor that has received study is the tangerine smell of the feathers of the Crested Auklet (*Aethia cristatella*; Humphrey and Phillips 1958, Hagelin et al. 2003; Figure 3l), which appears to aid the birds in forming and enforcing pair bonds (Jones et al. 2004, Hagelin et al. 2004). However, little is known about why or how these birds smell like tangerines. It is clear that the feathers carry the smell (Hagelin et al. 2003), but it is unknown whether the compounds are grown directly into the feathers or are cosmetically applied. Further research into this system should examine olfaction in mating in other species, such as the causes and potential roles of feather odorant compounds especially in communication and ectoparasite defense (Hagelin and Jones 2007), in the drepanidine Hawaiian honeycreepers (Pratt 1992), and other groups (Clayton et al. 2010) .

Chemical defense

Although toxic chemical defenses are present in all other classes of tetrapods, it was not until birds in the genus *Pitohui* were found to contain homobatrachotoxins in their feathers (Dumbacher et al. 1992) that chemical defenses were known in birds. These alkaloid toxins were originally assumed to be an anti-predator defense. Subsequently Poulsen (1994) suggested an anti-ectoparasite role for the toxin, although local people have provided evidence for the toxin to at least deter human consumption of these birds (Görlich 1995). Originally a single genus, *Pitohui* was subsequently found to be highly polyphyletic, and actually included species from three separate families (Jønsson et al. 2007, Dumbacher et al. 2008). The evolution of alkaloid toxin sequestration in the feathers of these distantly-related species may be examples of Mullerian mimicry (Dumbacher et al. 2008), or multiple realizations of an ancestral character through dietary convergence (Jønsson et al. 2007).

Cosmetic coloration

Once grown feather colors are generally fixed, as pigments, nanostructure, and microstructure cannot be altered. However, some species have evolved several mechanisms for modifying the feather coloration without molt. One mechanism is through the use of powder down, or pulviplumes. Many families of birds have special down feathers that can be easily pulverized by the bill and spread onto other feathers. These powders can contain pigments that are externally applied to other feathers by the bird, altering the apparent plumage color. Pulviplume powder is often white, but may also contain carotenoids (Thomas and McGraw 2018), imparting yellow, orange, or red colors. This method of cosmetic coloration is best known in the herons (Ardeidae), but appears to occur in other families of birds, including bustards (Otididae), cockatoos (Cacatuidae) and parrots (Psittacidae (Delhey et al. 2007).

In addition to feathers being ground physically into a cosmetic through structural degradation, modified pulviplume feathers (Peters et al. 2010) or apteria (Menon and Menon 200) can also secret lipoid fat (Peters et al. 2010), which can also used as cosmetic coloration through direct application to feathers, or by mixing with pulviplume powders. Lipoids mixed with pulviplume powders typically produce a yellow or orange color, which would stain white feathers when applied topically by the bird. Finally, secretions from the uropygial gland can be applied to feathers as cosmetic coloration. For example, Greater Flamingos (*Phoenicopterus roseus*) apply uropygial secretions containing carotenoid pigments to become more colorful (Amat et al. 2011).

Feather color can also be mechanically altered. Many bird species also alter their plumage through biannual molts between a more cryptic nonbreeding and a more colorful or gaudy breeding plumage, although the molts may have arisen simply to replace worn feathers and were only later co-opted for seasonal phenotype alteration (Pyle and Kayhart 2010, Wolfe 2011). Some species of birds (e.g. House Sparrow (*Passer domesticus)*, many New World blackbirds (Icteridae), and most notably the longspurs (Calcariidae)) alter their plumage patterns without molting, but instead use dimorphic feathers, in which a gaudy feather color is masked by a cryptic-colored feather tip. Through the year, these feathers wear down, and the overall color of the bird changes from a cryptic, generally brown plumage, to a bright and gaudy plumage used for sexual signaling (Leukering 2011).

3. Evolution of feather functions

In Section 2, we demonstrate that feathers have diverse functions involved in many aspects of avian biology, including locomotion, foraging, communication, and physiology. In this section, we examine both the evolutionary history of feathers, and how this critical avian trait has shaped the evolution and diversification of birds. We begin with an introduction to feathers as hierarchical modules, and define terminology for these modules. We discuss the evolution of feathers in archosaurs, the evolution of different hierarchical levels, gaps in our knowledge of the evolution of different hierarchical levels, the potential for the multifunctionality of feathers to facilitate evolutionary trade-offs, and how selection can act on intraspecific variation, variation across the body, or variation across feather hierarchical levels. We then examine the effects on functional evolution of molt as a means for renewing or altering feather functions, and finally review the developmental and genetic basis of feathers and how understanding this can contribute to our knowledge of functional evolution.

Hierarchical structure of feathers

Definition of Hierarchical Modules

A hierarchical model is one in which the most granular components are grouped into consecutively more cohesive units. An example of this is phylogeny, in which individuals belong to populations, populations can be grouped into species, species into clades, and so on. Feathers can be thought of as hierarchical modules with a combination of independent and covarying developmental controls (Prum and Dyck 2003). Because this complex hierarchical structure integrates aspects of feather morphology (i.e., integrating across patterning, barb morphologies, and barbule morphologies), birds produce new, complex phenotypes (Prum and Dyck 2003). Below, we define these hierarchical levels that build upon each other to create the diversity of functions described above (Figure 2, Figure 4). We start at the coarsest level, pattern, which contains all subsequent levels , and end at the molecular composition, the finest-scale, or most granular level. Note that these hierarchical levels described below exist within an individual bird, but these phenotypes are not static, and can change through time for an individual due to ontogenetic variation, molt, and wear (see Molt), or can vary among individuals of a population (e.g., sexual differences; see Evolutionary trade-offs and opportunity).

At the highest hierarchical level of the plumage phenotype, colors and patterns are constructed by all underlying variation across the entire body of a bird (Figure 2; reviewed by

Mason and Bowie 2020 and Inaba and Chuong 2020). Next, feather arrangement can be thought of as how individual feathers are positioned on the body of a bird, including feather tracts and pterylae, or bare areas (Lucas and Stettenheim 1972), and the density of feathers within these areas. At the level of the individual feather, developmentally controlled by feather placodes or follicles (Prum and Dyck 2003), we define macrostructure as consisting of the overall shape of the feather, including the pennaceous portion, plumaceous portion, afterfeather, and calamus (Lucas and Stettenheim 1972). Feather macrostructure can vary in the overall shape, presence or absence of these different feather components, or the proportion of the feather these components occupy. Feather microstructure is the variation in shape of each feather component - the rachis, barbs, ramus, barbules, and barbicels (Lucas and Stettenheim 1972). The shape of each of these components can vary within an individual feather (e.g., within the pennacous or plumaceous portions of the feathers), and these components can be present or absent, or vary in shape among feathers in different parts of the bird (e.g., contour feathers and flight feathers). We define the structure within each of these components to be the feather nanostructure, including variation in the cortex, keratin matrix, the size or position of air pockets (e.g., in larger vacuoles, or small, but regular air pockets within the spongy layer within a feather barb that produces structural color (Prum et al. 1998), and the size or position of melanocytes. Finally, the finest-scale level is the level of molecular composition, including pigments, elemental isotopes, and keratin. Pigments are molecules deposited within feathers that absorb specific wavelengths of light, and include melanins, carotenoids, psittacifulvins, porphyrins, spheniscins, and several unknown pigments (Lucas and Stettenheim 1972, Burns et al. 2017). Pigments can vary in molecular composition, concentrations, and locations of deposition. While the elemental isotopes incorporated into feathers are interesting for answering a number of different questions relating to different aspects of an organism's biology (e.g., Wiley et al. 2017), to the best of our knowledge, variation in elemental isotopes or molecular composition has not yet been linked to variation in feather function, so we will not address this type of molecular variation further. However, we acknowledge that variation at this level may have functional implications, so welcome future study.

Evolution of Hierarchical Modules

The hierarchical structure of feathers is not only represented in current avian biology but can be observed in feather evolutionary history. Feathers likely evolved as simple bristle-like integuments in early archosaurs and then diversified through increasingly complex structural differentiation (Prum 1999). Feathers existed mainly as body feathers on multiple lineages of dinosaurs (Xu 2006) diversifying in form and function mainly in the Therapoda and accelerating in structural evolution in Paraves and Aves (Ksepka 2020). As early birds evolved, feathers incorporated new functions, such as flight, through lengthening and stiffening of the rachis, hooklets that hold the vane closed, and asymmetrical barb length. These feather characteristics are all found in the flight feathers of *Archaeopteryx lithographica* (Bergmann et al. 2010). These flight feathers, along with bone structure, provide evidence that this early bird could fly; in addition to having separate regions of the body possessing functionally differentiated feathers. These regions of functional differentiation occurred at least as early as in *Microraptor gui,* from approximately 125 million years ago (Chatterjee et al. 2007). Because feathers evolved prior to birds, morphological combinations beyond those found in extant birds existed in the past, as has been demonstrated by the recent discoveries of novel Mesozoic feathers (Carroll et al. 2019, Wang et al. 2020). Little is known about archosaur or early bird feather microstructure, although some studies have identified fossilized melanin pigments and iridescent nanostructure (Vinther et al. 2008, Vinther et al. 2010, Hu et al., 2018).

Much of the focus on the evolution of feather functions has focused on feather colors, and plumage color evolution. Many studies analyze plumage color itself as a character, which may mask fine-scale, or interacting evolutionary signals. Feather color is a composite trait (Badyaev et al. 2001, Shawkey and D’Alba 2017), composed of variation in the hierarchical levels of a feather (Figure 2). Understanding the mechanistic underpinnings of these colors and how these mechanisms evolve across species is essential for untangling the selective pressures stemming from a variety of feather functions. With a few exceptions, studies have focused on the evolution of hierarchical mechanisms as contributors to coloration and associated functions, primarily involving communication. Below, we explain how different hierarchical levels are involved in color production, how analyzing color at different scales can reveal the effects of complex selection pressures, and finally, how some studies are beginning to consider the evolution of other feather functions at several different hierarchical levels.

As a first step, one way to quantify the mechanistic underpinnings of feather coloration at a gross level is by analyzing the shape of the reflectance spectrum (Dyck 1966). This method has been used to primarily categorize color production mechanisms into broad categories focused on the main mechanism - carotenoids, melanin, non-iridescent structural color, iridescent structural color, or structural white (i.e., Doucet et al. 2007). Analyzing this gross-level categorization of color can uncover remarkable patterns of color evolution. For example, Eliason et al. (2019) took a novel approach to understanding plumage color across a birds’ body by implementing biogeographic models over evolutionary time to understand how colors “move” across the bodies of kingfishers, and found that structural color seem to be more labile than pigment-based colors. However, the dichotomy between pigments and feather structure as underlying a coloration mechanism is misleading. While some colors are clearly a product of both pigmentary and nanostructural variation (D’Alba et al. 2012, Shawkey and D’Alba 2017), even colors that appear simply to be created by feather pigments are created by a combination of pigments and feather nanostructure (Shawkey and Hill 2005). Changes in either pigmentary or structural aspects of a color can produce variation in the gross-level appearance of the color or shape of the reflectance spectrum. This recognition highlights the importance of quantifying feather nanostructure and/or pigments to understand how the mechanisms that produce color evolve (Shawkey et al. 2009). For example, Maia et al. (2013) showed that the evolution of novel melanosome morphologies in starlings drove the evolution of iridescent coloration in the clade and was associated with varying rates of lineage diversification. Further, nanostructure variation is also correlated with aspects of ecology and behavior (Maia et al. 2016). Aspects of feather nanostructure are also associated with non-iridescent structural color variation in fairy wrens (keratin cortex, spongy layer, melanin layer; Fan et al. 2019) and Swallow Tanagers (Bazzano et al. 2021), and iridescent color variation in dabbling ducks (melanosome diameter, melanosome spacing, number of layers; Eliason et al. 2015) and hummingbirds (keratin cortex, melanosome variation; Eliason et al. 2020).

The above studies have clearly shown that pigments and feather nanostructure are important components of the feather hierarchical structure with variation linked to life history traits (Figure 4). However, variation in other hierarchical levels, such as feather microstructure, is increasingly being recognized as an important component of feather color variation. The structure of the rachis (Eliason and Clarke 2020), or microstructure of the feather barbs and barbules (Iskandar et al. 2016) can produce feather gloss, or a shiny appearance. Enlarged barbs can also enhance the chromaticity of colors (McCoy et al. 2021). Barbule microstructure can also alter color by absorbing light (McCoy et al. 2018), and “super black” plumage has evolved convergently in at least 15 different families of birds, using five different classes of barbule microstructure (McCoy and Prum 2019). Combinations of feather nano- and microstructure can also produce unusual effects in feathers, such as the mirror-like iridescence of the Lawe's Parotia (*Parotia lawsii*), which is produced by interactions between nanostructure in the barbules and the curved shape of the barbule (Stavenga et al. 2011). Feather microstructure is responsible for variation in hue at different angles even in non-iridescent structural colors or primarily pigmentary colors (Reed et al. 2020, Urquia et al. 2020). In brown and black feathers, feather microstructure has been shown to explain more variation in coloration than melanin content alone (D'Alba et al. 2014), highlighting the possible importance of microstructure in social signaling. It is clear that feather microstructure plays a role in avian feather production and must be studied in addition to the classically studied pigments and nanostructure to understand how color evolves.

Variation in feather morphology across hierarchical levels that does not play a role in color production has been largely overlooked in comparative studies of avian evolution. For example, downy plumage has clear implications for thermoregulation, but may not contribute to visual signals. Focusing on downy feathers, or downy aspects of feathers, Barve et al. (2021) showed that two measurements of feather macrostructure evolved to provide additional insulation - the proportion of the feather with downy barbs increased with elevation, and that feather length increased as body size decreased. Pap et al. (2020) found evidence for both measurements of feather macrostructure (e.g., feather size) and microstructure (e.g., barbule length and nodus density) were correlated with habitats that ranged from fully terrestrial to aquatic. Similar to how feather microstructure is increasingly recognized as important in color production, the evidence of feather microstructure contributing to other functions beyond social signaling highlights the importance of considering the evolution of these traits in a broader context. For example, feather barb roundness and complexity, and barbule density predict both visible and near-infrared reflectance (Igic et al. 2018, Stuart-Fox et al. 2018), and near-infrared wavelength reflectance is important for thermal protection (Medina et al. 2018). Beyond thermal functionality, the barbule variation associated with iridescence also increases feather hydrophobicity, making them less waterproof (Eliason and Shawkey 2011). These studies show the importance of studying feather morphology across hierarchical modules with a focus on their many diverse functions. Comparative studies of evolution should seek to link life history variation with comprehensive measures of feather morphology.

Evolutionary trade-offs and opportunity

The selective landscape consists of peaks and troughs of fitness, given variation in a trait. Traits occupy space on this landscape based on current variation, but have the potential to move throughout the fitness landscape as traits evolve. If a trait occupies a fitness peak and can only evolve through gradual, stepwise changes, selection would not favor the evolution of this trait to higher fitness peaks if it requires the traversal through troughs of lower fitness. However, Persons and Currie (2019) point out that feather evolution provides an example of how multiple separate axes of selection (e.g., sexual vs. natural selection) can help organisms “jump” across gaps between peaks in selective landscapes. However, this applies more broadly than with sexual vs. natural selection. Depending on their functions, feathers are under many different selective pressures at any one time, multiple of which may fall under the categories of sexual and natural selection. For example, a feather may function for thermoregulation, waterproofing, protection for other feathers, intersexual and intrasexual signaling, and crypsis simultaneously. These selective forces may push feather structure in similar or different directions, and the peaks of one adaptive landscape may bridge peaks of another, or reinforce isolation between landscape peaks. The multiple functions of feathers mean that feathers likely inhabit very complicated and high-dimensional selective landscapes. This means that there may be many unknown “peaks” in the selective landscapes of feathers, and novelty in feather structure can open up vast potential for morphological evolution for birds. For example, the evolution of tail spines in tree-climbing birds (Figure 3) can be found in at least three separate clades of bark-foraging birds (see *balance/bracing)*, and may be an essential trait associated with that ecological niche.

The evolution of feather function is key to understanding the diversification of birds, but much remains to be discovered about how feather function evolved and interacts with avian evolution. For example, what trade-offs are present when a novel function develops? Some functions, such as flight, appear to be reversible (James and Olson 1983), while other functions, such as protection from parasites may be more universal. Important questions to understand in the diversification of birds are: How do novel feather functions create novel adaptive space for birds? What are the limits of multifunctionality of feathers? How do separate selective forces interact to bridge gaps between selective regimes for other functions? How does a birds’ environment interact with novel feather function evolution? As an example, in warm environments, relaxed selection on thermoregulatory function in feathers may allow for broader functional diversification than in colder environments where birds cannot afford to compromise thermoregulatory function (Figure 5). Thus, environmental and life history factors may inhibit or encourage feathers to “explore" functional trait space for new adaptive peaks (Figure 3). Release from thermoregulatory needs may help explain the latitudinal diversity gradient in birds: with less pressure to perform a thermoregulatory role, feathers are free to evolve novel functions and lead birds down novel evolutionary and ecological space. For example, iridescent feathers show a reduced ability to repel water (Eliason and Shawkey 2011), which may explain the lack of iridescent feathers on the body plumages of many aquatic birds. Terrestrial birds may have lower pressure on plumage for water repellency, and thus are free to develop iridescent colors in response to sexual selection.

The hierarchical complexity of feathers not only has implications for our understanding of their evolutionary underpinnings (e.g. Prum 1999), but also may constitute a framework that is useful for understanding how feathers respond to the myriad of selective pressures associated with their multifunctionality discussed above. We hypothesize that these selective pressures may not actually operate on the composite character that is the plumage phenotype, but rather on individual hierarchical components across the avian body (Figure 4). Because of the multifunctionality of feathers, birds have evolved specialized feathers on different regions of the body, and every bird possesses an array of functional phenotypic diversity within its feathers (Figure 1). Most birds possess feathers that are specialized for flight in the remiges and rectrices, in addition to body feathers that are specialized for thermoregulation, waterproofing, and signalling, at a minimum. Recent work on feather specialization has concentrated especially on parsing the relative effects of sexual and natural selection on signaling in the form of coloration across birds' bodies (Maia et al. 2016, Marcondes and Brumfield 2019, Shultz and Burns 2017, Simpson et al. 2020, Dunn et al. 2015, see also review by Mason and Bowie 2020) and have found that light environment, habitat, and social systems play large roles in the evolution of feather colors across the bodies in birds. Thus, studies seeking to correlate the evolution of plumage with specific selective pressures should consider specific aspects of feather hierarchical morphology and the location of these feathers on the body rather than the phenotype as a whole. These hierarchical modules may enable species to explore novel trait space, while still being constrained by selection.

Understanding the complex landscape of selective pressures and how they shape the evolutionary history of feathers may be a daunting task. However, several promising avenues are promising for this purpose. Quantifying variation in feather morphology across hierarchical levels in phylogenetically and ecologically diverse species is one way to do this, as we discussed in the previous section. However, an alternative approach is to take an intraspecific approach, that is, to study the evolution of feather morphology as it varies among individuals in a population, potentially due to sexual differences or ontogenetic variation (variation among life stages). Here we focus on sexual differences, and expand upon ontogenetic variation in the Molt strategies section. This approach has already been shown to be important for understanding color evolution (e.g., Burns 1998, Shultz and Burns 2017, Dunn et al. 2015). In 2005, Shawkey et al. found lower barbule density in structural blue feathers in males than in females. Recently, Enbody et al. (2017) found that feather barbule morphology varied between males and females in two species of fairy wren, while overall patterning and pigmentation was similar. Taking an interspecific approach, McCoy et al. (2021) investigated feather pigmentation and microstructure in male and female *Ramphocelus* tanagers. They found that even though color patterns varied between sexes, this variation was largely due to microstructure and melanin differences, rather than differences in carotenoid pigmentation. Because this variation exists only in males and not in females, McCoy et al. (2021) implicate sexual selection in the form of dishonest signaling as responsible for these differences, but until the other functional implications (thermal, parasite protection, etc) of these microstructural differences are known, it is difficult to infer the true driver of this variation. Understanding how variation in feather morphology is constrained or can vary between sexes that share life histories, but have different breeding systems, may be a fruitful way to disentangle the selective pressures across hierarchical modules.

Molt strategies

The hierarchical structure of feathers may provide a means for multiple selective pressures to operate simultaneously, but there may be incompatible changes in functional needs across the lifetime or annual cycles of a bird. Change or maintenance of functions requires replacement of feathers through the process of molt. Molt interacts with feather function through both structural renewal and the opportunity for phenotype change in new feathers (Figure 6). Because of this, understanding molt strategies in birds is necessary to understand how feathers function and how these functions evolve. Different bird species show a variety of molt patterns (Stresemann and Stresemann 1966, Pyle 1997). Some hypotheses have been put forward that link the way birds use their feathers to the evolution of these molt patterns (Howell 2010, Pyle and Kayhart 2010, Wolfe 2011) and some studies have linked evolutionary process to patterns of molt (Bridge et al. 2007, Delhey et al. 2020, Guallar and Figuerola 2016, Guallar et al. 2020, Holmgren and Hedentröm 1995, Svensson and Hedenström 1999), as well as ecological processes influencing molt (Kiat et al. 2020a, Kiat and Izhaki 2020, Terrill 2018, Terrill et al. 2020, Wolfe et al. 2021). However, our understanding of the evolution of molt patterns in birds remains nascent compared to other life history characteristics of birds. The few studies that have examined the interactions between molt and feather function in an evolutionary context have found that molt strategies can be independent of a birds' ecology and evolutionary history, but can affect a species' evolutionary trajectory. The interaction between molt and avian evolution stems from the two major ways molt affects feathers: functional renewal, and phenotype alteration.

Molt: renewal of function

Molt serves to replace worn feathers (Figure 6). When a feather becomes worn, its function can be compromised and a new feather restores this function (Jenni and Winkler 2020). The need to maintain feather functions is, at the most basic level, the reason that birds molt their feathers, and molt strategies are likely influenced to some degree by selection on feather quality throughout the year. Another important aspect of feather function during molt is that the function of an individual feather is lost during molt, between the time the old feathers is discarded, and the time that the new feather has grown enough to perform functions (Rohwer et al. 2020). These two aspects of function during molt, renewal and temporary loss have likely guided the evolution of molt strategies, as well as the evolution of feather function. Temporary function loss affects avian evolution through the evolution of molt strategies to mitigate function loss, or, evolution of general adaptations to survive without feather function. Molt strategies that mitigate function loss include gradual molts, like the sequential molts seen in the wing feathers of many birds. These gradual molts avoid wing gaps that would compromise flight (Swaddle and Witter 1997), and birds that are more reliant on efficient flight for foraging appear to minimize the number of adjacent molting feathers (Bridge 2006, Chandler et al, 2010, Howell 2010, Shugart and Rohwer 1996). However, trade-offs do exist in molt timing, and there appear to be drawbacks to a protracted molt especially in birds in highly seasonal environments (Terrill 2018). These costs may include overlap of molt with migration (Benson and Winker 2015, Holmgren and Hedenstrom 1995), molting outside an ideal productive season (Tonra and Reudink 2018), and hormonal limitations. Birds are limited hormonally in their ability to mount an adrenal response to stressors, because corticosterone, the primary hormone that initiates this pathway, negatively affects feather quality during feather growth (DesRochers et al 2009), and must be downregulated during molt (Romero et al 2005). In addition, molt pace may also be affected by factors such as nutritional condition (Grubb 1989, Grubb and Cimprich 1990), home range size (Yosef and Grubb 1992) or foraging guild (Wolfe et al. 2021). How the trade-offs associated with molt timing interact with a birds' physiology and life history is an essential question to investigate in order to understand the evolution of feather function and molt strategies.

Some birds do undergo rapid molts and appear to evolve adaptations to mitigate loss of function during molt, instead of minimizing functional loss. For example, many species of birds undergo a simultaneous molt of the flight feathers on the wing, rendering these species flightless during the molting period (Stresemann and Stresemann 1966, Howell, 2010). These species appear to have evolved adaptations to allow them to forage and escape predators during molt. Terrill (2020) found that the lineages of birds with this synchronous molt show highly elevated rates of evolution of complete flightlessness, and hypothesized that adaptations for a temporary flightless period during molt serve as pre adaptations for complete flightlessness. This interaction serves to illustrate the complicated nature of evolutionary interactions between a birds' molt strategies and their evolutionary histories: molt strategies are both influenced by and have influence on a species' phenotype and life-history strategy over evolutionary time.

The interaction between molt strategy, phenotype, and life history may also serve to illuminate a species' life-history strategy or ecology, which can be useful for poorly-known or even extinct birds. Kiat et al (2020b) examined a fossil of *Microraptor* in active molt, and found that this individual was undergoing a sequential wing molt, much like many modern species of birds that rely on flight year-round. The authors argued that this molt strategy served as evidence that *Microraptor* was reliant on flight year round, likely relying on flight both for foraging and escaping predators. With the new increase in high-quality fossils with preserved feathers (Fucheng et al 2006), we hope that more specimens can be found in active molt, and that molt strategies in extinct birds and dinosaurs may serve to inform what we know about these extinct species. Understanding molt strategies in extinct archosaurs could potentially illuminate the evolution of function over the history of feathers.

The diversity of molt strategies in birds implies some sort of selection on molt strategies, and the presence of many species that have converged on similar strategies in similar environments implies potential strong selection on molt strategy by environment. For example, in the United States and Canada, many species of birds in the east undergo a prebasic molt before migration, just after breeding; and many species in the west undergo this molt during or after the fall migration (Rohwer et al. 2005, Pyle et al. 2009). Many pairs of sister species follow this east/west divide, and even closely related taxa within the same species show this molt timing divide. This may in fact be the strongest gradient of parallel adaptation across North America in birds, and implies strong selection on molt timing between eastern and western birds in this region. Understanding the nature and consequences of this selection may be informative to studies of speciation and hybridization within this region. For example, if selection on molt timing is strong and differential between the east and western areas of the United States and Canada, does this selection impose a postzygotic barrier to hybridization when a hybrid undergoes an intermediate or “incorrect” molt for its location? Furthermore, would this selection promote speciation by limiting parent individuals to their “appropriate” eco region, given their molt strategy; and by limiting hybrids to an intermediate region? These questions remain open, but may provide substantial insight into the dynamics of speciation and hybridization across this region.

Molt: change of function

The other basic way in which molt interacts with feather function is phenotype alteration (Figure 6). Here, we refer to phenotype alteration as a new feather that grows with a different phenotype than the feather that it replaced. Feather phenotypes can change seasonally or through ontogenetic maturation. Seasonal phenotype alteration is generally manifested through basic and alternate (“breeding” and “nonbreeding” plumages), though at least one taxon, the ptarmigans (Tetraonidae) undergo three molts a year, each producing a distinctive phenotype (Pyle 2007). Many species of birds show distinctive seasonal plumages, but our understanding of how and why seasonal plumages evolve remains poor. For example, seasonal plumages are thought to reflect differential selection on feather function throughout the year, but recent studies have focused on the evolution of biannual molts and seasonal phenotype change have found evidence for more complicated scenarios. In the New World warblers (Parulidae), Terrill et al. (2020) found that the evolution of biannual molt appears to be linked to long-distance migration, and hypothesized that feather wear plays a primary role in the evolution of a biannual molt. Biannual molt has to evolve before it can then evolve seasonal phenotype alteration. This scenario demonstrates the complicated relationship between phenotype change and functional renewal in the evolution of molt strategies, and serves to highlight how the evolution of molt strategies interacts with feather function. In this case, a molt strategy may have evolved in response to selection against worn feathers, but once present, can also serve as a mechanism for seasonal plumage alteration, and thus influence the evolution of coloration in these species. Because of the complicated nature of the interactions between molts, feather function, and phenotype; any study on the evolution of feather phenotype, including avian coloration, should consider how molts interact with feather phenotype over evolutionary time.

In addition to seasonal changes, feather phenotypes can also change through ontogenetic development. As birds mature, so do their feathers. The first feathers birds grow are downy feathers that function mostly for thermoregulation (Wetherbee 1957, Crome and Rushton 1975, Johnson et al. 1993). These feathers are quickly replaced by more adult-like contour and flight feathers of the juvenile plumage (Pyle 1997, Howell 2010), which are in turn replaced by fully adult-like feathers weeks to a year after (Guallar et al. 2020, Howell et al. 2003). In this way, the phenotypes and functions of feathers change throughout an individual’s first year of life. In some species, feather phenotype can continue to develop past the first annual cycle through delayed plumage maturation. Delayed plumage maturation has received a fair amount of research and theory, but, like in other aspects of feather evolution, these studies often fail to consider molt. Rowher and Butcher (1988) demonstrated how understanding molt is essential to understanding the evolution of delayed plumage maturation by showing that partial molt in first-year birds responds to winter selection, not selection on the breeding grounds. This is in contrast to other studies (Hawkins et al. 2012, Lyon and Montgomerie 1986, McDonald 1993, Studd and Roberston 1985) that propose adaptive mechanisms for delayed plumage maturation based on social interactions on the breeding grounds. These hypotheses are backed by substantial theory, but as with the evolution of seasonal plumage change (Terrill et al. 2020), the story appears to be more complicated when molt is considered. New research into delayed plumage maturation with high-quality spectral analysis has since found further evidence that selection away from breeding sites affects plumage maturation, even in highly social birds like the manakins (Pipridae) (Morales-Betancourt and Castano-Villa 2018). At the most basic level, molt is the mechanism by which plumage matures, and which feathers molt and when can inform our understanding of plumage maturation. Like with seasonal phenotype change, we suggest that molts be considered in any study of plumage maturation.

Genetic and Developmental Basis of Feather Composition

The extent to which the hierarchical nature of feathers can accommodate different, and possibly contradictory feather functions requires that these features have at least partially independent genetic and developmental controls. While many open questions still exist as to the genetic mechanisms that control the development of particular aspects of feathers, the application of genomic techniques have allowed huge strides in this area.

As discussed above, feathers evolved and diversified prior to the evolution of modern birds (Ksepka 2020), with some feather morphologies existing only in extinct lineages (O'Connor et al. 2012). The full complement of feather patterning genes were present long before the evolution of birds, in the amniote ancestor (Lowe et al. 2014), although some gene families may have contracted or expanded as archosaurs and later birds evolved (e.g. β-keratins; Greenwold and Sawyer 2013). While the coding regions evolved early, associated regulatory regions evolved later, with an estimated 86% of feather gene regulatory regions evolving in the ancestor of archosaurs (Lowe et al. 2015). Taken together, this suggests that the evolution of feathers in modern bird lineages is due to modifications of a toolkit that evolved before modern birds. The variation in feather morphology and associated functions explored above highlight the potential utility of comparative genomic approaches for understanding how this genetic toolkit has been modified to produce these diverse morphologies within modern birds. For example, Greenwold et al. (2014) demonstrated that the count and proportion of β-keratin genes vary across lineages with different life histories (e.g., aquatic and predatory birds). However, the lack of understanding of the genetic basis of diverse feather morphologies have limited the ability to connect feather phenotypes to genotypes and their underlying evolutionary history.

Major efforts are underway to understand the genetic basis of feather diversity using three main strategies - using developmental biology approaches on different feather morphologies, using domesticated species as models, and finally, comparing closely related species or populations that vary in plumage patterning (reviewed by Ng and Li 2018 and Price-Waldman and Stoddard 2021). Using developmental biology approaches, Ho et al. (2019) identified the molecular basis of feather arrays, and Bailleul et al. (2019) identified the developmental mechanisms associated with dorsal plumage patterning and feather tract formation in a diverse set of species. Chang et al. (2019) examined rachis and barb morphologies across species with diverse ecologies, and identified diverse rachis morphologies associated with different life history strategies (e.g., burst or sustained flight). Importantly, they also identified the developmental and molecular mechanisms associated with rachis modification, plumaceous vs. pennaceous barb identity, and barbule morphology (filamentous, plate, or hooklet shape) (Chang et al. 2019). This work is an important first step, but future work is needed to refine these findings and extend them to other barb and barbule morphological variation (e.g., downy feather morphological variation, Pap et al. 2020, superblack barbule architectures; McCoy et al. 2018). Reviewed by Saranathan and Finet (2021), little is known about the genetic control of feather nanostructure variation, although developmental studies have found that coherent scattering is likely produced by self-assembly of keratin and air channels both in feather barbs (producing non-directional coherent scattering; Prum et al. 2009), and a combination of guided and self-assembly in feather barbules (producing iridescent coherent scattering; Maia et al. 2011, Rubenstein et al. 2021).

While our understanding of the genes associated with feather structure across hierarchical levels is still in its infancy, many studies have informed our understanding of the genes involved in feather pigmentation, particularly facilitated by a combination of studies on domestic species, and high-throughput sequencing of bird populations (Reviewed by Funk and Taylor 2019, Ho et al. 2019, Price-Waldman and Stoddard 2021). Historically, most work has been conducted on the genetic basis of melanin pigmentation; MC1R was the first plumage coloration gene identified as responsible for changes in melanin pigmentation, with single nucleotide polymorphisms (SNPs) in coding regions associated with melanin-based plumage polymorphisms (Mundy et al. 2004, Mundy 2005, reviewed by Hubbard et al. 2010). A combination of candidate gene approaches and genome-wide data comparing rapid radiations or closely related populations highlight additional genes involved in melanogenesis pathways that are also involved in controlling melanin patterning and composition (e.g. phaeomelanin vs eumelanin production, agouti signaling protein (ASIP)) (Uy et al. 2016, Stryjewski and Sorenson 2017). Unlike for melanin coloration, the genetics of carotenoid coloration were unknown until recently (reviewed by Toews et al. 2017), with some major advances with high-throughput sequencing (e.g., the identification of CYP2J19, a gene involved in the yellow dietary carotenoids to red ketocarotenoids (Lopes et al. 2016; Mundy et al. 2016), or BCO2, a gene important in sex-specific carotenoid pigmentation in canaries (Gazda et al. 2020)). However, there is still a long way to go before we have an in-depth understanding of the integration of networks of genes with the metabolic networks of carotenoids that describe how carotenoids can be metabolized from one type to another (e.g., the networks identified by Badyaev et al. 2019). Finally, of less common avian feather pigments (Other feather pigment chapter of Hill and McGraw 2006), only psittacofulvins have been studied from a genetic perspective. The gene responsible for yellow psittacofulvin synthesis was identified using a genome-wide association study of budgerigar varieties (Cooke et al. 2017).

While the identification of genes associated with certain types of pigmentation is exciting, there is much work to be done to improve our functional understanding, and to study how they have evolved across populations and species. For example, Rodríguez-Martínez and Galván (2019) found that in Zebra Finches, social interactions had implications for the expression of a gene involved in phaeomelanin production. Nadeau et al. (2007) estimated strength of selection as measured by the ratio of nonsynonymous to synonymous substitutions (dN/dS) across Galliformes and found that dN/dS was correlated with the degree of sexual dichromatism. The expression of CYP2J19 was examined across weaverbirds, and while it was highly expressed in retinas across all species due to the importance of carotenoids in the visual systems of birds, it was also found to have increased expression in the liver in birds that had metabolically-altered carotenoids in their plumage. This implies that this gene may have been co-opted for use in the evolution of feather pigmentation from ancestral functions in the avian retina.

An additional link between feather genetics and phenotypes is hormones, which can be involved in regulating gene expression during feather development. Hormones interact with feathers in complicated ways, principally during the molting process. Hormones are understood to trigger molting (Hahn et al 1992), and the prebasic molt appears to be triggered through cascades that begin with drops in testosterone after the breeding season (Payne 1972). However, adjustments of timing of molt may be complicated. For example, when female White-crowned Sparrows were artificially kept in breeding condition, males were able to delay molt as well in response to this social cue (Runfeldt and Wingfield 1985). Hormonal replacement experiments (Perez et al 2018) and poultry science (Sekimoto et al 1987) support a direct role for the thyroid hormones triiodothyronine and thyroxine for induction of the prebasic molt. An important and unstudied question related to hormones and the timing of molt is how molt timing evolves. For example, when sister species undergo a prebasic molt before or after the fall migration, what controls this difference, and what are the mechanisms of evolution of the timing of molts? Additionally, it is important to understand the genetic and hormonal underpinnings of the evolution of separate molt strategies, for example, the evolution of inserted molts such as prealternate or presupplemental molts. In addition to influencing the timing of molts, hormones can also influence the condition and coloration of feathers. Corticosterone appears to negatively affect feather quality when it is present in the blood in elevated amounts during molt (DesRochers et al. 2009, Lattin et al. 2011), and is downregulated during molt (Romero et al 2005), presumably to improve feather quality. In addition, feather color appears to be at least partially controlled by hormones during molt, especially in species with sexual dichromatism. Hormonal interactions with feather coloration have been reviewed previously (Kimball 2006), and so we will only cover this topic briefly. In short, controls of sexual dichromatism appear to largely follow broad taxonomic groups, but more research is needed to determine if this is a true pattern or a result of patchy experimental work. Control of plumage coloration (regulation of gene expression) can be separated into hormonal and nonhormonal, though non-hormonal control of feather color is even more poorly understood than hormonal control. Hormonal control of molt can be further divided into three categories: estrogen dependence (Paleognathae, Galloanserae), androgen dependence (Charadriiformes, some Passeriformes), and luteinizing Hormone dependence (some Passeriformes) (Kimball 2006). Recent studies have tied hormone regulation to the expression of genes important in pigment regulation (Khalil et al. 2020), but more research is needed into the evolution of hormonal control of feather color, as well as the evolution of gains and losses of sexual dichromatism, seasonal dichromatism, and plumage maturation.

Together, all of this work demonstrates that while we are beginning to understand the genes coding for different aspects of feathers, much more work is needed to understand how these genes are regulated and eventually produce the diverse phenotypes described above. Many of these genes, especially those involved in pigmentation, are consistently showing up across whole-genome scans between closely related species and populations, or hybrid zones (Funk and Taylor 2019, Price-Waldman and Stoddard 2021). Functional testing and additional comparative genomic work (e.g., Sackton et al. 2019) can help connect these genes to the phenotypes they code for, and eventually contribute to an understanding of how this genomic toolkit evolves across birds.

Conclusions

1. Functions

Here we expand upon Stettenheim (1976) by outlining the functions of feathers. These separate functions are often quite distinct, for example flight and odor encompass different physical and behavioral processes for birds. These functions are produced by modifications on different aspects of the hierarchical nature of feather composition as well as changes associated with molt patterns. We review evolution of functional diversity, and explain how a holistic understanding of hierarchical structure, molt, and evolution is necessary to understand any one feather function.

2. Evolution of Functions

How exactly feather functions diversify over time requires research. The high amount of multifunctionality in feathers means that many functions have evolved repeatedly within structures that previously served for other functions. How and why the feathers that serve for thermoregulation may involve coloration, or flight ability, for example, likely has to do with trade-offs associated with reliance on previous function and the ability of feathers to perform both the old and new function. The costs and benefits of these trade-offs, as well as the mechanisms for the evolution of novel function, require much more research.

Despite the importance of feathers in bird biology, feathers evolved in the Archosaurs before birds. In this review, we cover the known functions of feathers in extant taxa, but recognize that this is only a snapshot of functional diversity over many millions of years of feather evolution. It is likely that additional feather functions have gone extinct along with the taxa that bore those feathers. We hope that paleontological data, especially from well-preserved specimens, may someday provide evidence for previously unknown feather functions from extinct species. Many dinosaurs had feathers, and inhabited ecological and behavioral niches beyond those of modern birds. Therefore, it is likely that to some extent, their feathers functioned differently than modern feathers. In addition to discovery of function, paleontological data can be combined with modern observations to illuminate behavioral or life-history characteristics of extinct species. For example, the observation of sequential molt in a fossil paravian suggests it was reliant on flight throughout the year (Kiat et al 2020).

The plumage phenotype is a composite trait, and needs to be considered to be made up of a series of hierarchical modules. Many studies have investigated the evolution of plumage colors and patterns, without considering the mechanisms that make up these traits. However, recent studies have started to investigate how hierarchical levels (e.g. microstructure, nanostructure, pigments) contribute to these composite phenotypes by studying both interspecific and interspecific variation. Future work should explicitly seek to disentangle the contributions of hierarchical modules to plumage phenotypes, by studying variation in multiple hierarchical modules simultaneously. Furthermore, future research should investigate how feather functions beyond social signaling are linked with evolution of feather morphologies across these hierarchical levels.

3. Molt Strategies

Molt strategies influence and are influenced by feather functions, likely in complicated ways. The diversity of molt strategies likely reflects trade-offs between needs for feathers and costs of feather growth, but surprisingly little research has investigated how and why molt strategies evolve. Future research should concentrate on how feather functions throughout the annual cycle influences the evolution of molt strategies -- but also how molt strategies may affect the evolution of feather functions. Furthermore, understanding molt strategies has influenced our thinking about the evolution of traits such as plumage maturation, sexual dichromatism, and seasonal dichromatism. We recommend that any study regarding feather function -- including feather coloration -- consider how molt may influence feather evolution.

4. Genetic and Developmental Bases of Feather Composition

The rise of high throughput sequencing has spurred the ability to uncover the genomic and developmental basis of feather morphology. Comparative genomics has shown that the genetic toolkit responsible for feathers evolved before birds, with most variation in modern bird feather phenotypes evolving through regulatory regions. Population genomic studies are uncovering the genes underlying plumage variation, especially those associated with pigments. Including developmental work with genomic studies is a powerful tool in not only discovering genes responsible for aspects of feather morphology, but to demonstrate the functions of these genes. Future work should seek to include more functional testing with genome scans, and to try and gain a better understanding of how these genes are regulated (including hormonal control). Furthermore, much work still needs to be done on understanding how genes evolve in conjunction with traits and life histories.

5. Synthesis

Feathers perform many functions for birds. Here, we identify at least 28 functions that feathers perform, many of which contain sets of functions that are performed simultaneously or through separate mechanisms. The implications of this high level of multifunctionality are that feathers allow for ecological and life-history diversification in birds, and that at any one time, a feather is performing multiple functions. Because of this, the evolution of a feather function may not be reflective of natural selection on a single function of focus, but instead be the product of a complex landscape of selection, acting on all functions of a feather across the annual and life cycles. For example, many studies have investigated feather color, but feather color evolution may be guided as much by interactions between colroation and thermal aspects, flight ability, or waterproofing; as by natural selection on color itself. In addition, molt strategies may either facilitate or limit feather functions. For example, molts may change a feathers' phenotype to adapt to variable selective pressures within the year, but birds can only perform the energetically expensive process of molting a limited number of times in a single year. Based on this review, we propose five basic questions for researchers to consider when studying the evolution of any feather function:

1) What additional functions are the feathers performing outside of the focal function?
2) What are the mechanisms that perform each function, and on which hierarchical level do they exist?
3) How do the separate functions interact, if at all? Do functions place morphological constraints on the feathers?
4) How do these functions vary in association with environmental or behavioral variation, either in an interspecific or intraspecific context?
5) What are the molt strategies of the birds of interest, and how may these molts interact with the focal function and other functions of feathers?

With these questions in mind, we believe research into feather evolution and feather function will gain more nuanced insight into evolutionary processes.

Acknowledgments:

We thank Matt Brady, Dr. Christopher Clark, Oscar Johnson, Dr. James M. Maley, Dr. John C. McCormack, Dr. J.V. Remsen, Jr., Dr. Kevin Burns, Dr. Dakota McCoy, Rosalyn Price-Waldman, Michael Tofflemire, Sarah Hood, Ben Scott, and Dr Jessica Anne Oswald Terrill for comments and assistance with the preparation of this manuscript.

Glossary:

Vane: The closed, flat section of a pennaceous feather, composed of barbs.

Rachis: The tubular central shaft of a feather within the feather vane.

Proximal: Referring to the direction towards the body on wings or feathers.

Distal: Referring to the direction away from the body on wings or feathers.

Calamus: The section of the rachis proximal to the vane.

Barbs: Branching structures off the rachis that form the vane.

Ramus: The tubular central shaft of a feather barb; plural is rami.

Barbules: Shafts the branch out from feather barbs.

Barbicels: Small hooks on the sides of barbules which connect the barbs to form a feather vane.

Rectrices: The primary, secondary, and tertial flight feathers of a bird; articulated to the carpometacarpus and ulna, respectively.

Remiges**:** Flight feathers articulated to the pygostyle that form a birds' tail.

Hierarchical modules: Nested physical structures of varying sizes.

Molts: The shedding and regrowth of feathers.

Annual Cycle: The cycle of hormonal, breeding, migratory, or molt events within the year.

Life History: Encompasses all factors that may affect when and how a bird invests time and energy in reproduction vs. survival.

Pigments: Chemical compounds which infer color to a feather or skin.

Nanostructure: Physical arrangement of keratin and pigment molecules within a feather. Refracts light to produce what is often referred to as "structural color".

Iridescence: A color that changes hue depending on viewing angle.

Figures

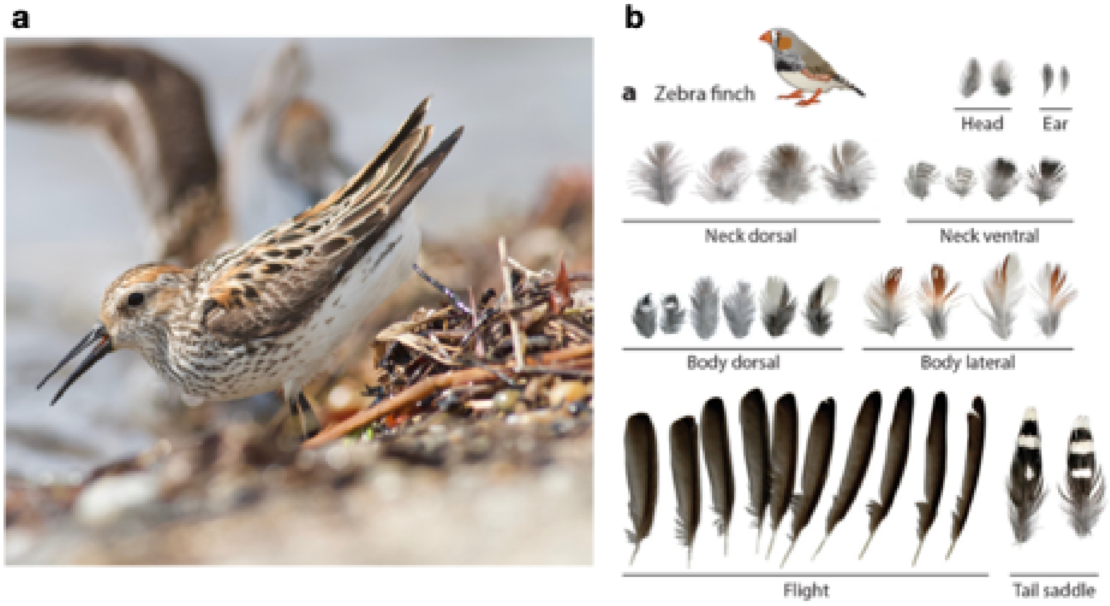

Figure 1. The phenotypes of birds’ feathers across their bodies represent a mosaic of functional trade-offs from competing selective forces. The molts and morphology of feathers within individual birds can respond to many separate forces through minor changes in feather growth ontogeny. For example, this Western Sandpiper (*Calidris mauri)* shows feathers that may be functioning for crypsis, mate choice, species signalling, thermoregulation, waterproofing, flight, and protection. These separate, competing forces all shape the diversity of feathers across and even among individual birds. Feathers from regions of a Zebra Finch (b) illustrate the morphological and functional diversity of feathers in one individual bird. Credits: a: RST, b: Reproduced from Chen et al 2015.

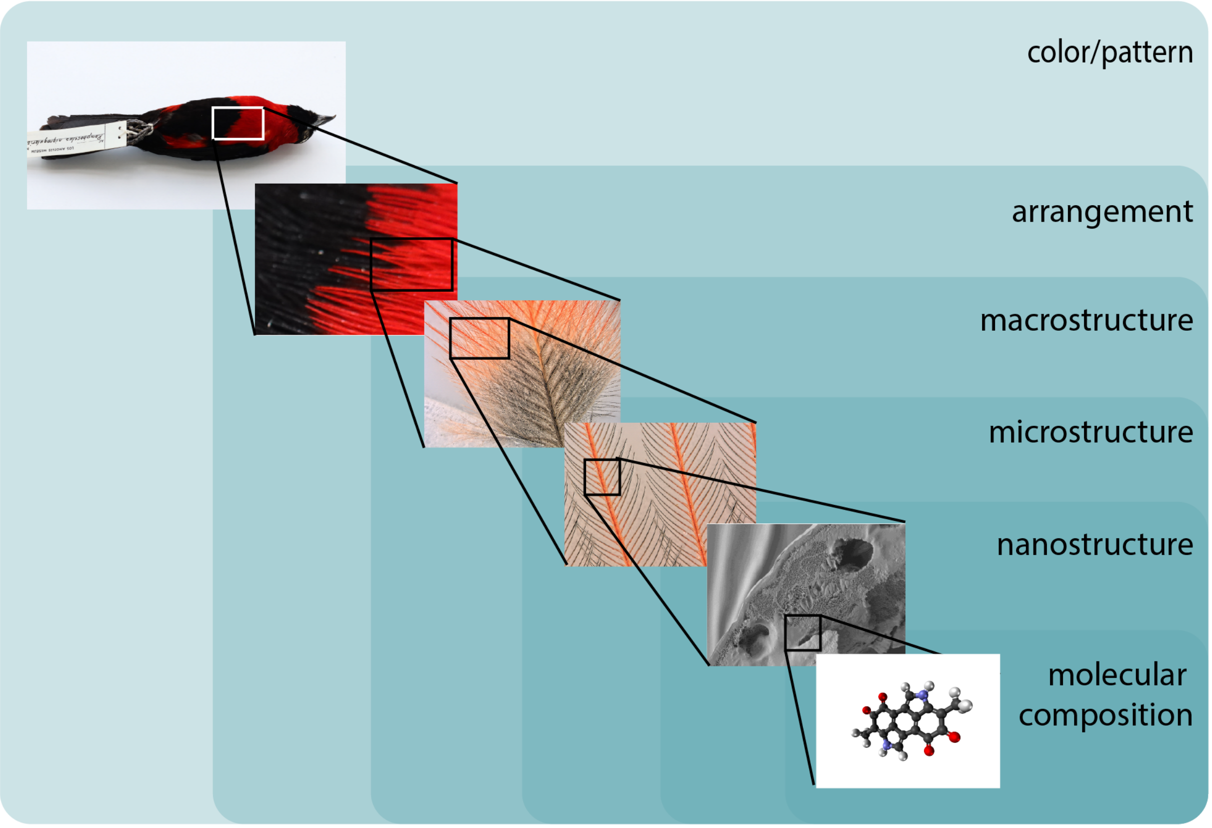

Figure 2. Plumage phenotype is composed of hierarchical modular levels, ranging from the color/pattern, to molecular composition. Each hierarchical level incorporates all previous component hierarchical levels. Photos for color/pattern and arrangement were taken by AJS at the Natural History Museum of Los Angeles County using *Ramphocelus sanguinolentus*, photos for macrostructure and microstructure were taken by Jacqueline Dall at the Natural History Museum of Los Angeles County using *Ramphocelus flammigerus*, and the photo for nanostructure is a Superb Fairywren barb cross-section taken by Nicholas M. Justyn, and the melanin illustration was created by Mhotep (Wikimedia commons, CC Share Alike 4.0).

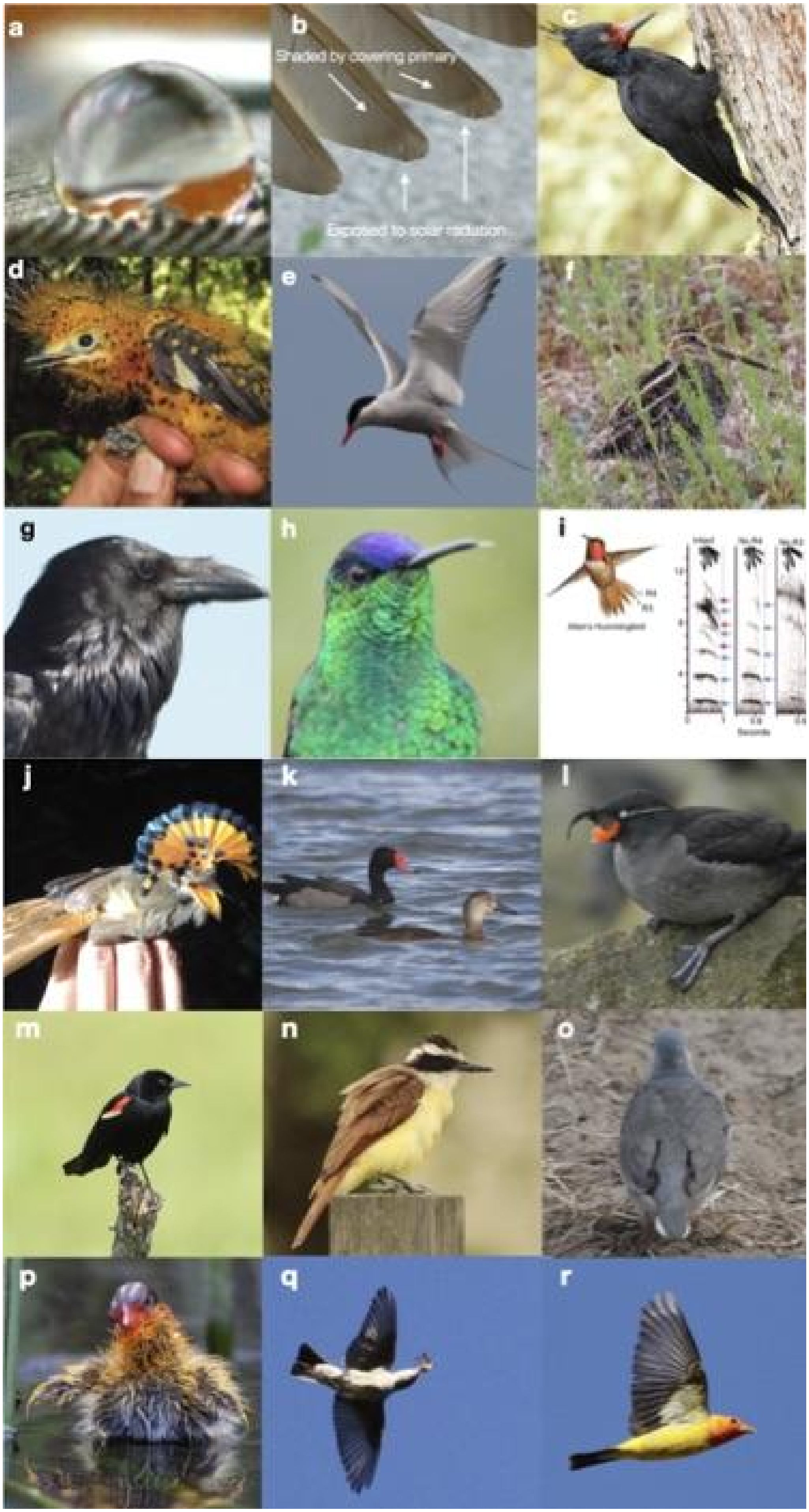
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Figure 3. Examples of some functions of feathers. a) Waterproofing is achieved through feather microstructure that causes water to bead up as opposed to penetrate a feather. b) Feathers protect other feathers. In the primary feathers of this Great Crested Flycatcher (*Myiarchus crinitus*) "shading" can be observed where each feather protects the feather below, and the exposed tips of the feathers are much more faded from solar radiation. c) Some groups of birds have stiffened rectices that aid them in balance during foraging, like this Magellanic Woodpecker (*Campephilus magellanicus*). d) The chicks of at least two species of Cotingas appear to be Batesian mimics on toxic caterpillars in their juvenile plumage. e) Feathers used in flight by this Arctic Tern (*Sterna paridisea)* help it fly both through achieving and disrupting lift, which helps it forage acrobatically in the air. f) Crypsis is achieved in many birds through outline disruption and background matching, like in this Wilson's Snipe (*Gallinago delicata*). Bristles often cover the nares or eyes of birds, as in this Common Raven (*Corvus corax).* These bristles may help protect sensitive orifices during foraging. h) Brilliant colors in tropical birds serve for dazzling sexual display. i) the tail feathers of hummingbirds in the "bee" clade often create mechanical sounds used in sexual displays. j) Bright feathers may serve to distract or disorient predators, as in this Royal Flycatcher (Onychorhynchus coronatus). k) Feathers increase a birds volume with negligible increase to mass, which makes most birds very buoyant; conserving energy of birds that live on top of the water. l) Some birds' feathers give off distinctive odors, as in this tangerine-smelling Crested Auklet (*Aethia cristatella).* m) Badges, like the red epaulets on this Red-winged Blackbirds (*Aegelaius phoenecius*) are often important signals for male-male competition. n) Many birds appear to engage in evolutionary mimicry of feather pattern and

color; and many unrelated flycatchers have converged on the overall phenotype of this Great Kiskadee (*Pitangus sulphuratus)*. o) Feathers wear in the sun, and birds' coverts protect essential flight feathers from added wear. When a birds' wing is folded, the flight feathers are mostly hidden underneath coverts, as in this Picui Ground-Dove *(Columbina picui*). p) Bright plumages interact with avian evolution in many ways: one is in parental choice, as in this chick American Coot (*Fulica americana*), which have been shown to receive food from their parents proportionally to plumage brightness compared to siblings. q) Flight serves many purposes in birds, including the ability to pursue and capture aerial prey, like this Olive-sided Flycatcher (*Contopus cooperi).* r) Flight also makes long-distance annual migrations possible, as in this Western Tanager (*Piranga ludoviciana*).

Credits: a) reproduced from Bormashenko et al. 2007. b) Jared D. Wolfe/Louisiana Bird Observatory. c) Luiz Moschini/MacCaulay Library d) reproduced from Londoño et al. 2015. e,h,j,k,m,n,o,q,r) RST. i) photo by Anand Varma, reproduced from Clark et al. 2011. l) Steve Tucker. p) Bruce Lyons.

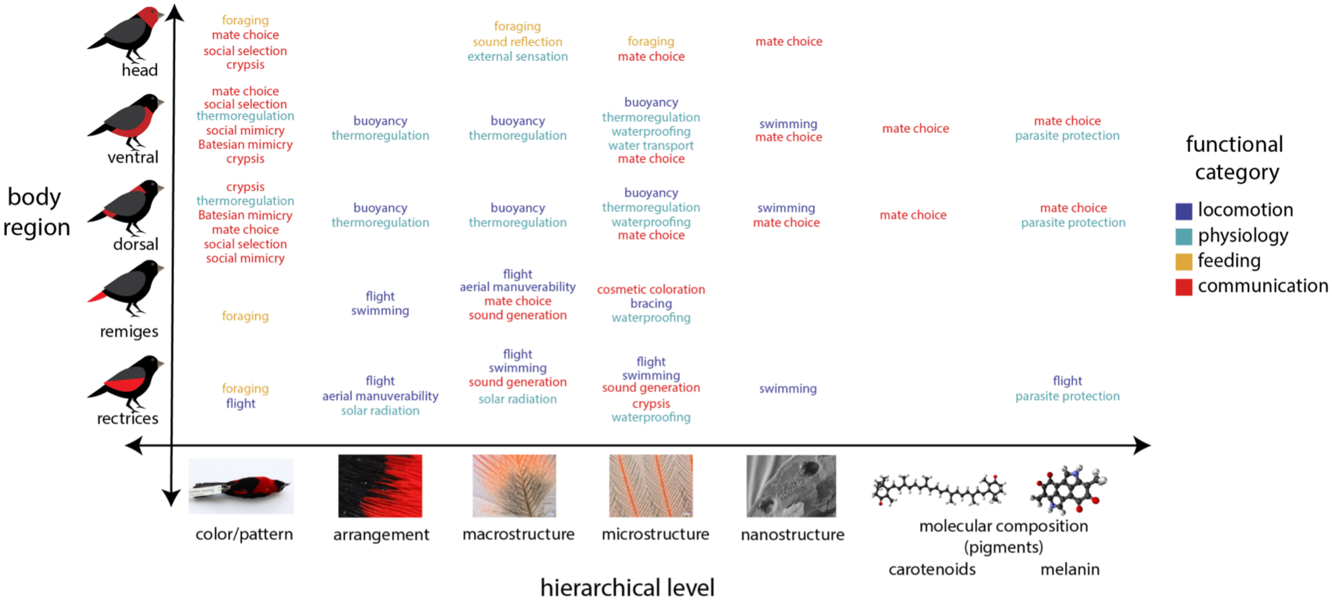

Figure 4. Feather functions (Section 2) identified as being produced or associated with specific hierarchical levels across regions of the body colored by overarching functional categories. Hierarchical levels range from the coarsest level, color/pattern, to the most specific level, molecular composition (here represented by pigments). Each hierarchical level can occur in different regions of a bird's body, which we describe here as the head, ventral region, dorsal region, remiges (tail feathers), and rectrices (wing feathers). Photos for color/pattern and arrangement were taken by AJS at the Natural History Museum of Los Angeles County using *Ramphocelus sanguinolentus*, photos for macrostructure and microstructure were taken by Jacqueline Dall at the Natural History Museum of Los Angeles County using *Ramphocelus flammigerus*, and the photo for nanostructure is a Superb Fairywren barb cross-section taken by Nicholas M. Justyn, the carotenoid (canthaxanthin) illustration was created by Jynto (Wikimedia commons, CC0), and the melanin illustration was created by Mhotep (Wikimedia commons, CC

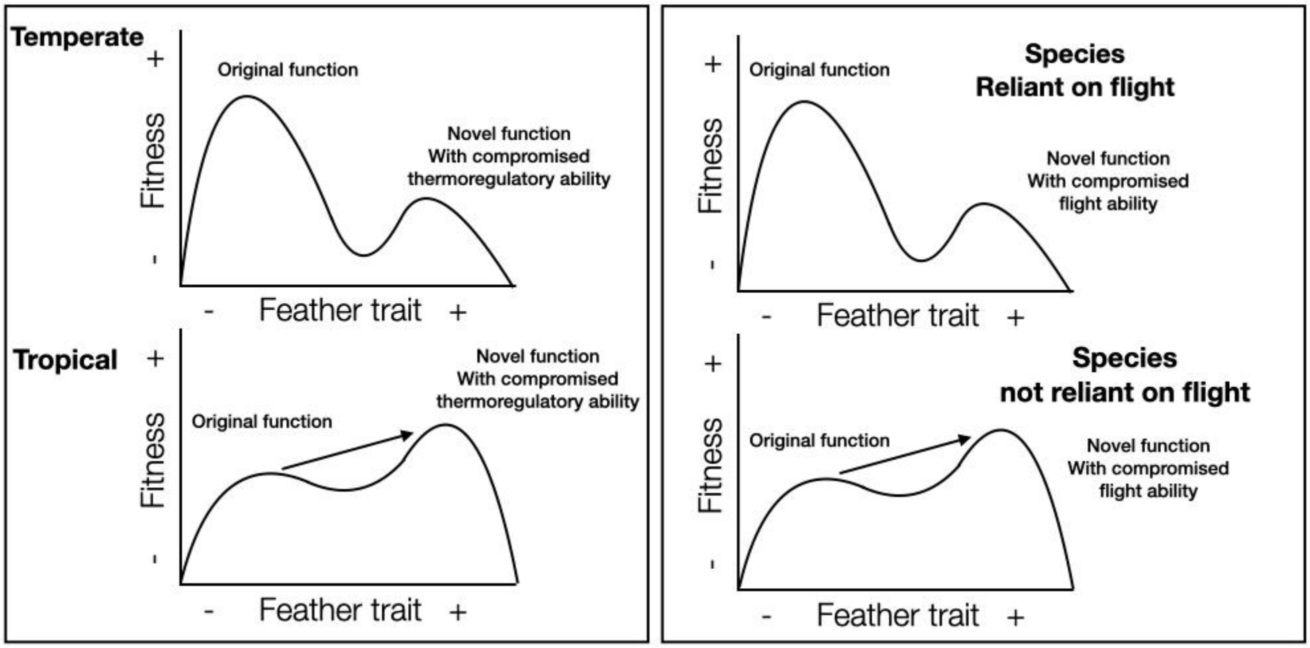

Figure 5. Examples of how environment and life-history may affect evolution of feather function over time. The availability of novel functions depends on both how the novel functions may compromise the original function, as well as the relative need for the original function. For example, birds with lower thermoregulatory needs in warm environments may be more free to explore feather functions that compromise thermoregulatory ability. Similarly, birds less reliant on flight may be able to develop novel functions for their wing feathers, such as swimming in

penguins (Spheniscidae).

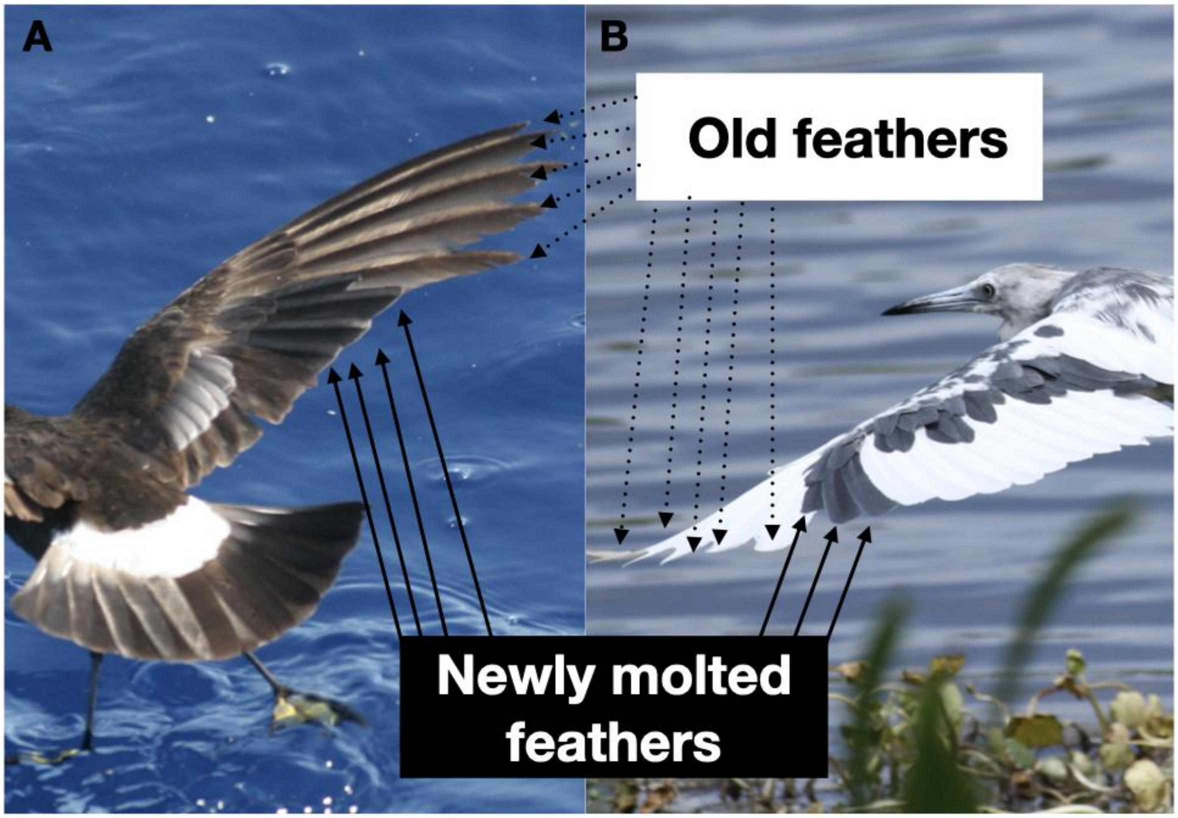

Figure 6: The dual purposes of feather molt. All birds molt their feathers annually, but molt can perform two distinct functions for feathers. Molt can replace worn or degraded feathers with fresh feathers to renew structural function like in this Wilson's Storm-Petrel, replacing faded and degraded flight feathers with fresh, new feathers (A). Additionally, molt can alter phenotype by replacing feathers with one color, pattern or shape with new feathers that differ, as in this young Little Blue Heron (B) replacing its white juvenile feathers with blue feathers of the adult phenotype. How these two functions of molt interact to influence the evolution of feather functions is a relatively new and poorly understood question that is likely fundamental to understanding the evolution of feathers and their functions, especially flight, thermoregulation, and coloration. Both photos: Ryan S. Terrill

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