



INVITED PAPER

Constraint and Function in the Predefinitive Plumages of Manakins (Aves: Pipridae)

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Synopsis Birds with delayed plumage maturation exhibit a drab predefinitive plumage, often despite gonad maturation, before developing the definitive plumage associated with increased reproductive success. Manakins are a diverse clade of neotropical lekking birds with extreme sexual dichromatism, radical sexual displays, and a unique diversity in the predefinitive plumages of males across species. Here, we provide the first full review of the natural history of manakin predefinitive plumages as the basis for qualitatively addressing the six major hypotheses about the production and function of predefinitive plumages. We find little evidence to support the possibilities that manakin predefinitive plumages are directly constrained by inflexible molt schedules, resource limitations to definitive coloration, or hormonal ties to reproductive behaviors. There is little evidence that could support a crypsis function, although direct experimentation is needed, and mimicry is refuted except for one unusual species in which predefinitive males sire young. Instead, evidence from a handful of well-studied species suggests that predefinitive plumages help young males explicitly signal their social status, and thereby gain entry to the social hierarchies which dictate future reproductive success. Our conclusions are especially influenced by the unique fact that males of at least 11 species throughout the family exhibit multiple predefinitive plumage stages with distinctively male patches. For each hypothesis, we highlight ways in which a better knowledge of female and young male birds offers critical opportunities for the use of manakins as a model clade.

Introduction

Beyond their mesmerizing beauty, avian plumages play fundamental roles in the sexual, social, and ecological lives of birds. These roles can range from attracting mates (Safran and McGraw 2004) to hiding from predators (Haskell 1996). In addition to the considerable functional and aesthetic diversity of plumages across species, and between the sexes of sexually dichromatic species, many bird species also show age-related plumage variation. In particular, some birds exhibit delayed plumage maturation, whereby young birds—often with otherwise mature gonads—molt into a drab “predefinitive” plumage before molting into the oftentimes more colorful “definitive” plumage associated with increased reproductive effort and success (Hawkins et al. 2012; Howell and Pyle 2015).

Evolutionary, ecological, and behavioral research on birds has begun to distinguish the various constraints on, and functions of, predefinitive plumages (Hawkins et al. 2012). Results have ranged widely across clades. For example, predefinitive plumages in some shorebirds result from the evolution of a unique juvenile plumage in combination with constraints against the evolution of an additional molt to replace those feathers (Chu 1994). In contrast, the predefinitive plumages of polygynous lekking satin bowerbirds (*Ptilonorhynchus violaceus*) functionally reduce male–male aggression during sexual and social interactions (Collis and Borgia 1993). As McDonald (1993a) notes, the ecology and evolution of predefinitive plumages will vary along with the broader ecology and evolution of different taxa of birds.

Manakins (Aves: Passeriformes: Pipridae) are small neotropical birds known for their extreme sexual dichromatism and gymnastic courtship displays (Kirwan and Green 2011). Male breeding plumages are colorful and high-contrast in most but not all species, whereas female plumages are largely green and drab (Doucet et al. 2007b; Ribeiro et al. 2015). Reproduction is usually centered around polygynous leks in which female choice for sexual displays can heavily skew male reproductive success (DuVal and Kempenaers 2008; Ryder et al. 2009). The extraordinary male sexual displays in this clade range from the coordinated, cooperative male jumping displays of the blue manakin (*Chiroxiphia caudata*, Foster 1981; Ribeiro et al. 2019) to the solitary, stridulating wing songs of the club-winged manakin (*Machaeropterus deliciosus*, Bostwick and Prum 2005). Delayed plumage maturation also varies across the family, including unique sequences of male predefinitive plumages that can progress across multiple breeding seasons (Ryder and Wolfe 2009).

In this paper, we present a qualitative review of manakin predefinitive plumages with a focus on three possible constraints to definitive plumage development (molt, resource, and hormonal constraints) as well as three possible functions of predefinitive plumages as signals (mimicry, crypsis, and status-signaling functions). We synthesize data on molt and feather development to address the constraint hypotheses and consider a wide array of ecological and behavioral studies to address the function hypotheses. Our integration of natural history and empirical evidence allows us to reason about hypotheses of both constraint and function, as well as address broader issues in development, physiology, signaling, and trait macroevolution.

Natural history of manakin predefinitive plumages

An example of manakin delayed plumage maturation is shown in Fig. 1, focusing on a subspecies of white-crowned manakins (*P. pipra pipra*) from a Brazilian population, as detailed by Johnson and Wolfe (2017). Males have a definitive plumage with a bright white crown and fully black body, wings, and tail. This male plumage is “definitive” in the sense that it has reached a stasis; all future molts will result in a similar plumage (Howell and Pyle 2015; but see Wolfe et al. 2014). Females in this population have a different definitive plumage—olive green across the wings, body, and tail, with some gray in the face—that is achieved after the first year.

In contrast, male *P. pipra pipra* will take more than 2 years to achieve their definitive plumage. Like other manakins, this subspecies has a “Complex Basic” molt pattern (Howell et al. 2003). This molt pattern involves a single, annual, and complete “prebasic molt” in all years except the first. In the first year of life, there is an incomplete “preformative molt” during which the bird sheds most of its juvenile plumage.

Soon after hatching, males begin their lives as fledglings in a dull green juvenile plumage (not shown). Approximately 2 months after hatching, fledglings undergo the preformative molt that replaces all feathers except for some juvenile wing feathers. This plumage closely resembles the definitive plumage of females, except for retained, worn, and duller green wing feathers. The timing of both molt and breeding varies across months, even within a single region (Johnson and Wolfe 2017).

The technical name of the plumage that arises from the first preformative molt is “first cycle formative” (previously known as “first basic”; Wolfe et al. 2014). This plumage appears identical across male and female *P. pipra pipra*. In contrast to the male definitive plumage, we refer to this plumage in males as “Stage 1 predefinitive.”

Male manakins appear to develop sperm-producing gonads capable of reproduction during this first year (e.g., *Chiroxiphia* spp.: Foster 1987; *Ilicura militaris*: M. Anciães unpublished data). Preliminary analysis of museum specimens suggests that mature testes are ubiquitous in predefinitive-plumage male manakins (R. Prum, unpublished data). In general, however, successful male reproduction appears to be delayed until a manakin transitions to its definitive plumage (but see the “Mimicry” section).

During the first breeding season after hatch, male *P. pipra pipra* initiate a complete “prebasic molt” that will replace all feathers from the Stage 1 predefinitive plumage. The resulting Stage 2 predefinitive plumage is usually green in the wings and tail with a medium gray head. These males can also have variable amounts of sporadic grayish-white feathers on the crown and gray feathers on the breast and belly (Johnson and Wolfe 2017). The corresponding prebasic molt in females results in the female definitive plumage.

About 1 year later, following the end of the second breeding season after hatch, males will undergo another complete prebasic molt. The result of this prebasic molt is the striking, black-and-white definitive plumage. Following this schedule, male white-crowned manakins are not available to breed in a

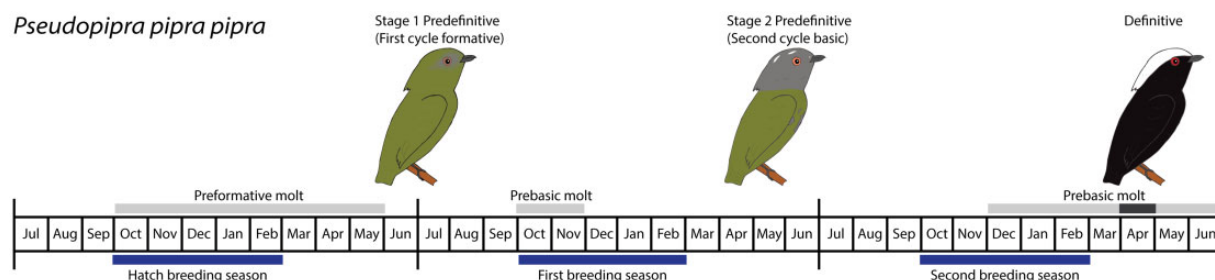


Fig. 1 Idealized summary of plumage and molt in a population of male White-crowned Manakins (*Pseudopipra pipra pipra*) near Manaus, Brazil following the data of Johnson and Wolfe (2017). Breeding seasons are based on the population rather than the breeding status of the focal bird. Males are not in their definitive breeding plumage until the third breeding season if they molt into this plumage following the second breeding season after hatch. Subsequent prebasic molts result in the same definitive plumage. The male Stage 1 predefinitive plumage resembles the female definitive basic plumage in this population. Grey bars indicate months during which captured birds were molting (Johnson and Wolfe 2017). Data is sporadic for the first two molts, whereas more consistent data for the definitive prebasic molt suggests a peak (darker bar) in April.

definitive plumage until the start of their third breeding season after hatch.

Table 1 summarizes the corresponding information for all other manakin species. Across 53 species, there are positive reports of delayed plumage maturation in 38 species. Although their gonads likely mature within the first year, these males will not breed in definitive plumage until at least their second breeding season after hatch. In at least seven species of manakins, males are known to molt from a single, female-like, Stage 1 predefinitive plumage into the definitive male plumage before their second breeding season. This single-stage, female-like predefinitive plumage pattern is likely much more general. We expect it will apply to many of the dichromatic species with no reports, as well as many of the 18 species that have confirmed delayed plumage maturation but lack both clear plumage descriptions and clear reports of multiple stages.

In at least 11 species, males exhibit one or more additional, predefinitive stages over successive prebasic molts that are progressively less female-like but not entirely definitive. In these species (except in the genus *Chiroxiphia*), Stage 1 predefinitive plumages are female-like and lack any distinctively male plumage patches.

The most complicated patterns are found in the genus *Chiroxiphia*. Male long-tailed manakins (*Chiroxiphia linearis*) do not molt into their definitive plumages until approximately 39 months after hatching, meaning they are not in a definitive plumage until the fourth breeding season. In addition, *Chiroxiphia* manakins have distinctively male red crown patches even in their Stage 1 predefinitive plumages. Though some definitive-plumage females show red crown feathers, female patches can be distinguished from those of predefinitive and definitive

males (Doucet et al. 2007a). Interestingly, males in this genus form especially complex, structured hierarchies that dictate reproductive opportunities (Foster 1981; Trainer et al. 2002; McDonald 2007; DuVal 2013), a fact which hints at an association between predefinitive plumage and social behavior (see the “Status-Signaling” section).

There were only four species with direct reports of an absence of delayed plumage maturation, all of which are sexually monochromatic (Table 1). Some monochromatic species of *Neopelma* and *Tyrannetes* manakins had no reports, although there is no indication that they differ from the monochromatic *Neopelma* known to lack delayed plumage maturation. None of the sexually monochromatic species are known to have delayed plumage maturation, and none of the dichromatic species are known to lack delayed plumage maturation. In species such as the green manakin (*Cryptopipo holochlora*), the evolutionary loss of sexual dichromatism is associated with a loss in lekking behavior (Ribeiro et al. 2015). While the explicit role that plumage has played in this joint evolutionary process is currently unclear, this loss presents an interesting opportunity for further research.

Eleven species completely lack published information about delayed plumage maturation. Of these missing species, the orange-crowned manakin (*Heterocercus aurantiivertex*) and the opal-crowned manakin (*Lepidothrix iris*) may be especially important. Unlike other unknown taxa, these species are only sexually dichromatic in a few plumage patches (Ribeiro et al. 2015). In combination with data from sexually monochromatic species, a closer look at the status of predefinitive plumages in these taxa could help reveal how predefinitive plumage evolution across species tracks sexual differences within species.

Table 1 Summary of available data on male manakin delayed plumage maturation and predefinitive plumages

Taxon	SD	DPM	DBS	Predefinitive descriptions	References
<i>Tyranneutes stolzmanni</i>	0	NR			
<i>Tyranneutes virescens</i>	1*	+		[P1]: Partial or absent yellow crown	JW
<i>Neopelma pallescens</i>	0	—			KG
<i>Neopelma chrysocephalum</i>	0	NR			
<i>Neopelma aurifrons</i>	0	—			KG
<i>Neopelma chrysolophum</i>	0	NR			
<i>Neopelma sulphureiventer</i>	0	NR			
<i>Chloropipo flavicapilla</i>	1*	+		[P1]: Duller yellow head	Hellmayr (1929); KG
<i>Chloropipo unicolor</i>	1	+		Uncertain: Scattered black on head, throat, and breast, followed by black across body	KG
<i>Antilophia bokermanni</i>	1	+	2+	Uncertain: Orange-red on crest and mantle followed by white patches on body	Azevedo-Júnior et al. (2000); KG
<i>Antilophia galeata</i>	1	+		Uncertain: Red on forecrown, superciliary, mantle, along with scattered black on breast. Later spotty red across mantle and upper scapulars, black tail coverts, and scattered black on body	Allen (1893); Marini and Cavalcanti (1992); KG
<i>Chiroxiphia lanceolata</i>	1	+	3	[P1]: Red “V” on crown; [P2]: Red crown and black on face; [P3]: Fuller red crown, black on face, scattered blue on back, scattered black on body, darker wings, tail [J]→[P1] 0–3 mos; [P1]→[P2] 10–12 mos; [P2]→[P3] 13–15 mos; [P3]→[D] ~26 mos	DuVal (2005)
<i>Chiroxiphia linearis</i>	1	+	4	[P1]: Red “V” on crown; [P2] Fuller red crown, black on face, occasional black on body, wing, tail; [P3]: Full red crown, black on head, body, wings, tail, scattered blue on back [J]→[P1] 0–4 mos; [P1]→[P2] ~15 mos; [P2]→[P3] ~27 mos; [P3]→[D] ~39 mos	Doucet et al. (2007a)
<i>Chiroxiphia pareola</i>	1	+	3	[P1]: Red/yellow on crown, black on face; [P2]: Previous plus blue on back, black on body	Cárdenas-Posada et al. (2018)
<i>Chiroxiphia boliviana</i>	1	+		Uncertain: Red on crown, scattered black on head, neck, breast, followed by some blue on back	KG
<i>Chiroxiphia caudata</i>	1	+	3	[P1]: Orange-red forecrown; [P2]: Red crown and black on face; [P3] Previous plus blue on breast, belly, undertail coverts, and rump [J]→[P1] ~3 mos; [P2] before 15 mos; [P3] before 27 mos; [D] before 39 mos	Mallet-Rodrigues and Dutra (2012) [includes detailed information on substages]
<i>Ilicura militaris</i>	1	+			Anciães et al. (2005)
<i>Masius chrysopterus</i>	1	+		[P1]: Female-like; [P2] Yellow on forecrown, black tips on hindcrown; [P3]: Yellow forecrown, wings, and tail,	Taylor et al. (2020)

(continued)

Table 1 Continued

Taxon	SD	DPM	DBS	Predefinitive descriptions	References
<i>Corapipo altera</i>	1	+	3	flattening red/orange feathers on crown, patchy black on body [P1]: Female-like; [P2]: Black on face, whiter throat with developing ruff [P1]→[P2] 15–19 mos; [P2]→[D] 27–30 mos	Jones et al. (2014)
<i>Corapipo leucorrhoa</i>	1	+	3	[P1]: Female-like; [P2]: Black on face, whiter throat [P2] before 15 mos; [D] before 29 mos	Rosselli (1994)
<i>Corapipo gutturalis</i>	1	+	3	[P1]: Female-like; [P2]: Black on face, whiter throat [P2] before 15 mos; [D] before 29 mos	Prum (1986); Aramuni (2019); JW
<i>Xenopipo uniformis</i>	0	—			Snow (2020a)
<i>Xenopipo atronitens</i>	1	+		Uncertain: Black on crown, lores, ears, wings before filling in face, throat, scapulars, breast	KG
<i>Cryptopipo holochlora</i>	0	—			Wetmore (1972)
<i>Lepidothrix coronata</i>	1	+	3	[P1]: Female-like; [P2]: Blue crown, variable black across body [P1]→[P2] ~2 mos; [P1]→[P2] ~14 mos; [P2]→[D] ~26 mos	Ryder and Durães (2005); KG
<i>Lepidothrix nattereri</i>	1	+		Uncertain: Brighter yellow belly, undertail coverts and some white on crown	KG; Snow and de Juana (2020)
<i>Lepidothrix vilasboasi</i>	1*	+		Uncertain: Brighter green wings and yellow belly, yellow on rump, uppertail coverts, green-gold on crown and nape with darker forecrown	KG
<i>Lepidothrix iris</i>	1*	NR			
<i>Lepidothrix suavissima</i>	1	+		Uncertain: Some patchy black	Hilty (2003); Snow (2020b)
<i>Lepidothrix serena</i>	1	+		Uncertain: Some patchy black	Prum (1994b); Snow (2020c)
<i>Lepidothrix isidorei</i>	1	NR			
<i>Lepidothrix coeruleocapilla</i>	1	+		Uncertain: Blue on crown and nape	KG
<i>Heterocercus aurantiivertex</i>	1*	NR			
<i>Heterocercus flavivertex</i>	1	+	2+	[P1]: Female-like	Prum et al. (1996); KG
<i>Heterocercus linteatus</i>	1	+		Uncertain: Orange-red crown, dull white throat	KG
<i>Manacus candei</i>	1	+	2	[P1]: Female-like [P1]→[P2] before 5 mos; [D] before 15 mos	Wolfe et al. (2009)
<i>Manacus aurantiacus</i>	1	NR			
<i>Manacus vitellinus</i>	1	+	2+	[P1]: Female-like	Day et al. (2006)
<i>Manacus manacus</i>	1	+	2	[P1]: Female-like (with possible UV differences)	Morales-Betancourt and Castaño-Villa (2018), Tu et al. (2020); JW
<i>Pipra aureola</i>	1	+		Uncertain: Red on crown, face, breast	KG
<i>Pipra filicauda</i>	1	+	3	[P1]: Female-like; [P2]: Yellow on forehead, red on crown and nape	Ryder and Durães (2005); KG

(continued)

Table 1 Continued

Taxon	SD	DPM	DBS	Predefinitive descriptions	References
<i>Pipra fasciicauda</i>	1	+		[J]→[P1] ~2 mos; [P1]→[P2] ~14 mos; [P2]→[D] ~26 mos <i>Uncertain</i> : Red on breast, ears, crown, followed by red, yellow, black on body	Robbins (1985); KG
<i>Machaeropterus deliciosus</i>	1	NR			Kirwan and Snow (2020) Kirwan (2020)
<i>Machaeropterus striolatus</i>	1	+			
<i>Machaeropterus eckelberryi</i>	1	+			
<i>Machaeropterus regulus</i>	1	NR			
<i>Machaeropterus pyrocephalus</i>	1	+		<i>Uncertain</i> : Female-like with variable golden-yellow on forecrown, reddish throat	Hilty (2003), KG
<i>Pseudopipra pipra</i>	1	+	3	[P1]: Female-like; [P2, <i>pipra</i>]: Gray on head with variable white on crown and gray on body [P2, <i>cephaleucos</i>]: White crown, slate gray face and belly [P2, <i>separabilis</i>]: Medium gray crown, gray face, and lighter gray belly [J]→[P1] ~2 mos; [P1]→[P2] ~14 mos; [P2]→[D] ~26 mos	JW; Berv et al. (2020) [includes taxonomic variation]
<i>Ceratopipra cornuta</i>	1	NR			Wolfe et al. (2009); KG
<i>Ceratopipra mentalis</i>	1	+	2	[P1]: Female-like (variation: orange-red on head, scattered black on body, dusky tertials)	
<i>Ceratopipra erythrocephala</i>	1	+	2	[J]→[P1] ~5 mos; [P1]→[D] ~17 mos; [P1]: Female-like (variation: yellow traces on crown, scattered black on body) [J]→[P1] ~3 mos; [P1]→[D] ~15 mos	JW
<i>Ceratopipra rubrocapilla</i>	1	+	2+	<i>Uncertain</i> : Red around eyes, variable black on body	Castro-Astor et al. (2004)
<i>Ceratopipra chloromeros</i>	1	+	2+	[P1]: Female-like	Tello (2001)

Notes: Blank cells indicate missing data. SD indicates sexual dichromatism (0 = monochromatic, 1 = dichromatic, 1* = limited dichromatism) as scored by Ribeiro et al. (2015). DPM indicates evidence for delayed plumage maturation (+ = positive evidence, – = negative evidence, NR = no reports). DBS indicates the first definitive breeding season (i.e., the first breeding season after hatch during which a male would be in a definitive plumage). Predefinitive descriptions include a summary of available information about plumage stages, including the timing of molts (→) between stages in months since hatch ([J] = juvenile plumage, [P#] = stage # predefinitive plumage; [D] = definitive plumage). Descriptions marked *uncertain* could represent distinct plumage stages, molting birds, or rare variants. KG = Kirwan and Green (2011), JW = Johnson and Wolfe (2017).

Many important details are also missing for species that do have confirmed delayed plumage maturation. Our earlier summary for *P. pipra pipra* was made possible only because of detailed recapture records for one population (Johnson and Wolfe 2017). Some species, especially those in the genus *Chiroxiphia*, have similarly detailed records (DuVal 2005; Doucet et al. 2007a; Mallet-Rodrigues and Dutra 2012). Other species, such as the golden-winged manakin (*Masius chrysoterpis*), have information about the sequence of discrete plumage

stages but not about timing (Taylor et al. 2020). Still other poorly known species, such as the black manakin (*Xenopipo atronitens*), are known to have delayed plumage maturation only from the examination of museum specimens (Kirwan and Green 2011). In these latter cases, available reports make it impossible to determine whether uncertain plumage descriptions capture discrete stages, transitions between stages, or unusual variants.

One important benefit from more precise predefinitive plumage descriptions will be a better

understanding of variation within species, subspecies, and even populations. As noted above, male *P. pipra pipra* exhibit variable white and gray feathers in their Stage 2 predefinitive plumages, and males can even show scattered green feathers in their early definitive plumages (Johnson and Wolfe 2017). Similar variation has been observed in other species, including one male golden-winged manakin that retained the same predefinitive plumage stage across more than 15 months (R. Prum, unpublished data).

Some intraspecific variation may be the result of multiple species or subspecies being collapsed into a single description. For instance, our summary of *P. pipra pipra* plumages represents just one population of the current nominate subspecies from what could be a suite of up to 17 distinct species (Berv et al. 2020). Recent *Pseudopipra* descriptions point to differences in predefinitive plumages, especially in *P. pipra cephalucos* and *separabilis* (Table 1). Ample plumage variation exists in other polytypic species, most notably in blue-crowned manakins (*Lepidothrix coronata*, Reis et al. 2020). Understanding this variation will be critical not only to avoid confusion, but also because intraspecific variation in molt and plumage forms the natural basis for the evolution of delayed plumage maturation. With this caveat in mind, we next apply the available reports on manakin predefinitive plumages to the major hypotheses that consider their production and function in ecological and evolutionary contexts.

Constraint hypotheses

One explanation for drab predefinitive plumages is that young birds are incapable of, or constrained from, expressing the definitive plumage that would otherwise offer reproductive or other benefits. There are at least three kinds of constraints which could result in a predefinitive plumage: molt constraint (which limits the growth of new feathers), resource constraint (which limits the development of particular kinds of feathers), and hormonal constraint (which binds the expression of definitive plumages to the deferred expression of social and sexual behaviors). Below, we address these constraints for manakin predefinitive plumages. We discuss empirical evidence opposed to all three constraint hypotheses and suggest research questions to further probe the roles of constraint in plumage evolution.

Molt constraint

In species with partial molts, the qualities of a predefinitive plumage may be the result of retained

feathers rather than the development of new predefinitive feathers. One form of molt constraint involves the evolution of a non-definitive juvenile plumage, combined with a retained partial molt between the juvenile and first basic plumages (Chu 1994). The result is a first basic plumage that is predefinitive only because it retains some non-definitive juvenile feathers. A second form of molt constraint involves the evolution of a non-definitive basic plumage for the winter, combined with a retained partial molt into a subsequent “alternative” plumage for the summer (Rohwer and Butcher 1988). The result is a first alternative (summer) plumage that is predefinitive only because it retains some first basic (winter) feathers. As Hawkins et al. (2012) argue, the presence of a molt constraint is not evidence against selection for a particular life history strategy. However, molt constraints can be one clue that predefinitive plumages have not evolved via selection, narrowly, for a given predefinitive plumage.

Our survey of manakin plumage and molt does not support a molt constraint hypothesis. No manakin predefinitive plumages are predefinitive only insofar as they retain some juvenile feathers. All male manakins grow fresh green feathers in their Stage 1 predefinitive plumages. In *Chiroxiphia* spp., Stage 1 plumages also include the growth of a new red crown patch. Further, no plumages beyond the Stage 1 predefinitive are constrained by partial molts in any species, as there are complete molts between subsequent basic plumages. Finally, manakins lack an alternative breeding plumage and thus a constrained molt between winter and summer plumages cannot apply.

Although manakin predefinitive plumages do not appear to be governed by molt constraints, understanding molt patterns is still a critical area of research. Of particular interest is the variation in the duration and modularity of molts across taxa. How flexible is the evolution of new molts, or differences in molt timing within annual cycles? For example, Mallet-Rodrigues and Dutra (2012) carefully characterize eight distinct plumage stages in blue manakins where a complex basic molt pattern expects only three molts. To what extent can prolonged plumage succession be controlled by a single molt? Alternatively, have some manakins evolved inserted molts that allow for more precise transitions between stages? A better understanding of the duration and precision of molt in species such as blue manakins will guide us in these evolutionary questions.

Resource constraint

Whereas molt constraints restrict whether birds can grow new feathers, resource constraints restrict the kinds of feathers that can grow. For example, Hill (1996) proposed that delayed plumage maturation in *Haemorrhous* finches is an evolved, canalized response to the underlying production costs of red plumage produced with carotenoid pigments. Three main modes of feather coloration—structural coloration, melanin pigments, and carotenoid pigments—differ in terms of the relevant limits in development. Structural coloration is produced by optical interactions between light and keratin, melanosomes, and air (Prum 1999), in addition to pigments (Shawkey and Hill 2005). Although studies have proposed correlations between various types of avian structural coloration and condition (White 2020) there is still no known mechanism through which the structural barb-rami colors (the anatomical type found in manakins) could be resource-limited beyond feather development itself. For example, the gleaming crowns of definitive male opal-crowned (*L. iris*) and snow-capped (*Lepidothrix nattereri*) manakins are produced via matrices of keratin and air within barbs (Igic et al. 2016). Indeed, some green plumage of female *Lepidothrix* is itself produced with structural elements (Saranathan et al. 2012). These are simply the constituent components of all barbs, with an organization precipitated by spongy medullary cells and self-assembly (Prum et al. 2009). Resource limitations to feather development might structure the evolution of particular molt schedules (Hahn et al. 1992), but are presently incapable of explaining why a young manakin would grow entirely new feathers lacking definitive coloration.

Melanin pigments are also unlikely to be a limiting resource for the eumelanin, and to a lesser extent pheomelanin, patches of definitive male manakin plumages. The main precursors of melanin pigments are amino acids that birds can synthesize themselves (McGraw 2003). Although minerals such as calcium are required for proper melanin deposition, no studies have demonstrated environmental limitations in precursors relevant to wild bird populations (McGraw 2008; Roulin 2016).

In contrast, research has more clearly investigated possible limits in the carotenoid pigments with which birds produce reds, oranges, and yellows (Svensson and Wong 2011). Birds must obtain carotenoid pigments directly from their food and allocate this resource not only to feathers, but also to immune and antioxidant systems (Koch and Hill 2018). For manakins, the relevant prediction is that

carotenoid plumage patches should be the limiting factor in predefinitive plumages. Non-carotenoid patches should develop more quickly or more fully toward the definitive state.

Wherever carotenoid pigmentation is present, manakin predefinitive plumages are inconsistent with a carotenoid limitation. All manakins with carotenoid plumage patches develop them before, or in conjunction with, any melanin or structural patches (Table 1). For example, the Stage 1 predefinitive plumages of *Chiroxiphia* feature a carotenoid-pigmented crown set against an entirely green plumage (or simultaneous with a black mask). In golden-winged manakins, the Stage 2 predefinitive plumage is olive green with a yellow carotenoid forecrown. In taxa with female-like predefinitive plumage stages, variants generally exhibit carotenoid elements before or simultaneously with other definitive patches (e.g., *Ceratopipra mentalis*). Even taxa with poorly-known plumage patterns follow a carotenoid-first pattern. For example, uncertain descriptions of helmeted manakins (*Antilophia galeata*) specify the appearance of red feathers on forecrown, superciliary, and mantle in advance of definitive black body feathers (Kirwan and Green 2011).

Research suggesting that carotenoid plumage patches are signals of nutritional condition or immunological status has largely relied on evidence from temperate, granivorous finches (e.g., Hill 1992; McGraw and Ardia 2003). In contrast, frugivorous manakins forage for the abundant, conspicuous, and carotenoid-rich fruits of the tropics (Snow 1971). Studies of bare-part coloration in other birds confirm that even immune-suppressed individuals can maintain their colors when carotenoids are readily available (Saino et al. 2000; Baeta et al. 2008). Diet scarcity is only one kind of limitation that has been suggested for condition-dependent carotenoid signals (Olson and Owens 1998). Koch and Hill (2018) reject external resource limitations for carotenoids, and instead argue for internal limitations in the conversion and allocation of pigments. However, the persistent detail that young, non-breeding manakins develop carotenoid patches first seems unlikely to support any straightforward hypothesis for predefinitive plumage evolution based on such limitations.

Hormonal constraint

If the same hormonal systems mediate plumage and behavior, these systems can tie the evolution of predefinitive plumages to the evolution of reproductive behaviors (cf., Hau 2007). Of particular interest are the androgen and estrogen chemicals which play

broad roles in sexual development. Seasonal gonadal growth in birds is structured by the expression of gonadotrophin-releasing hormones from the hypothalamus, resulting in production of androgen or estrogen steroids from the gonads (Ubuka et al. 2013). Seasonal expression of these steroid hormones helps modulate key reproductive behaviors in birds, such as singing and courtship (Schlinger and Brenowitz 2002; Fusani 2008).

At the same time, sex steroid hormones can play diverse roles in the expression of sex- and age-specific plumages (Owens and Short 1995; Kimball 2006). For example, androgens induce male and female definitive plumages of the sexually monomorphic black-headed gull (*Chroicocephalus ridibundus*, Groothuis and Meeuwissen 1992). Sex steroid hormones are also associated with intraspecific, intrasexual variation of both melanin (Evans et al. 2000) and carotenoid (Stoehr and Hill 2001) plumage patches. On the other hand, evidence from some passerines has shown that plumage development can be linked to luteinizing hormones from the pituitary rather than steroid hormones from the gonads, or can be more generally non-hormonal (Kimball 2006).

In cases where a shared hormonal mechanism mediates both reproductive behaviors and definitive plumages, selection against reproductive behaviors in young birds, in the form of selection against hormonal expression, could result in the evolution of delayed plumage maturation. From this perspective, the evolution of predefinitive plumages would be the result of evolutionary constraints on the hormonal ties between plumage and behavior rather than the result of selection for a specific functional plumage (Ketterson and Nolan 1999; Hau 2007).

Evidence from a handful of manakin species suggests that androgen expression and reception is tied up with male reproductive behaviors (*Chiroxiphia lanceolata*: DuVal and Goymann 2011; *Manacus vitellinus*: Schlinger et al. 2013; *Pipra filicauda*: Ryder et al. 2020). However, experiments on golden-collared manakins (*M. vitellinus*) have shown that testosterone implants do not induce definitive male plumage, even though the implants induce courtship behaviors in predefinitive males (Day et al. 2006). This result aligns with the fact that male manakins can develop capable testes well before definitive plumages (see especially Foster 1987). Although direct physiological evidence is limited to one species, the evidence shows that some manakin predefinitive plumages can evolve independently of reproductive behaviors with respect to androgen expression.

The lack of a hormonal connection between definitive plumage and reproductive behavior in golden-collared manakins contrasts with evidence from other birds with delayed plumage maturation. For example, testosterone implants in young satin bowerbirds were associated with intrasexual aggression, display behaviors, and male definitive plumage development (Collis and Borgia 1993). How does predefinitive plumage evolution differ between birds that have hormonally unlinked plumage and behavior and those that maintain this link? How freely has this link evolved, within and across avian clades? Future research into the hormonal mechanisms of delayed plumage maturation will help answer broader questions about the shifting role of developmental systems as mediators of macroevolutionary patterns.

Functional hypotheses

Rather than being the product of developmental or environmental constraints, manakin predefinitive plumages may have functional signaling properties with direct benefits to survival or reproductive success. Three major hypotheses have been proposed for predefinitive plumage function (Hawkins et al. 2012): crypsis, whereby drab plumages help birds evade detection by predators; mimicry, whereby young birds are allowed in rival territories because they appear female or juvenile; and status-signaling, whereby plumage explicitly signals lower reproductive or subordinate social status in order to diminish aggression by competitors or gain access to developmental opportunities. We discuss these hypotheses in light of manakin natural history and behavior. Our review of the evidence finds little support for the role of mimicry or crypsis, instead suggesting that status-signaling is the major functional element of predefinitive plumages for at least a few well-studied taxa.

Crypsis

The crypsis hypothesis states that drab predefinitive plumages help inexperienced young birds remain inconspicuous and thus evade predation (Selander 1965; Rohwer 1978). In birds, few studies have shown that predefinitive plumages serve a crypsis function (Hawkins et al. 2012). The prediction of this hypothesis is that predation rates should be higher for definitive-plumaged males than predefinitive-plumaged males of the same age. Testing the hypothesis would likely require direct experimental manipulations of plumages (e.g., Berggren et al. 2004), but this experiment has not been done with manakins.

Although it is not direct evidence against crypsis, we note that 11 species have male predefinitive plumages with colorful patches. Indeed, this fact is true of all known Stage 2 and subsequent predefinitive plumages. While these patches can be drab (e.g., the gray head of some *P. pipra pipra* Stage 2), they can also include colors ranging from red (e.g., *P. filicauda* Stage 2) and yellow (e.g., *M. chrysopterus* Stage 2) to blue (e.g., *C. linearis* Stage 3). Colorful patches potentially disfavor predator avoidance as they can be in high contrast with leks' background environment, especially during displays and when seen from short distances (Endler and Thery 1996; but see Anciães and Prum 2008). An attempt to also render these patches as an anti-predation adaptation (e.g., as indicators of "unprofitable prey," Götmark 1992) would have to appeal to additional sensory ecological mechanisms that are fundamentally different from crypsis.

Hawkins et al. (2012) suggest that crypsis benefits can be a sort of general assumption for drab plumages. Extending this argument, one might assume that a crypsis function of female definitive plumages would readily apply to young male manakins in female-like plumages. However, for at least 13 dichromatic manakin species, there are periods during which plumage but not behavior or life history is shared between females and young males. In terms of behavior, young males from a wide array of species practice displays, both alone and with other males (e.g., Tello 2001; Castro-Astor et al. 2004; Cárdenas-Posada et al. 2018; Schaedler et al. 2020, 2021). Such behaviors could readily attract predators. In terms of life history, annual adult survival rates (across ages and plumages) are high in many manakin populations (McDonald 1993b; Blake and Loiselle 2002; Pearce-Higgins et al. 2007), whereas egg- and nest-predators appear to be a more major threat (Foster 1976; Ryder et al. 2008a; Reidy 2009). Drab, displaying males could be vulnerable to adult predation just as drab females remain inconspicuous to nest predators. While available studies do not refute crypsis, any support for the evolutionary dynamics of predefinitive crypsis must account for the unique contexts of females and young males.

Mimicry

The mimicry hypothesis posits that predefinitive plumages help young males be mistaken for females (Rohwer et al. 1980) or juveniles (Foster 1987), thereby reducing aggression from older males when mimics enter territories in search of breeding opportunities or information about habitat quality.

Research on mimicry is largely based on temperate migrants for which establishment in high-quality breeding territories is fundamental to reproductive success (Hawkins et al. 2012). Given that tropical food resources are widely available outside of lek display territories, the benefits of mimicry for a young male manakin would likely come in form of breeding opportunities. The mimicry hypothesis therefore predicts that (1) conspecifics cannot differentiate predefinitive males from females or juveniles and (2) mimics should gain some reproductive success.

Males in predefinitive plumages are unlikely to be effective mimics of females. Although many predefinitive plumages resemble female definitive plumages, at least 11 species have stages with patches that would clearly distinguish young males from females. Stuffed models experiments confirm that male long-tailed manakins do not display for, or copulate with, Stage 1 predefinitive plumaged models—the most female-like stage, albeit with a red crown patch—in contrast to usual interactions with females (McDonald 1993a). It is also unlikely that predefinitive plumages are effective juvenile mimics. Males and females of all species molt into first cycle formative plumages that differ from the drabber juvenile plumages held for only a short time (see especially Johnson and Wolfe 2017).

Even when plumage alone might fool a conspecific, the common display behaviors of young male manakins readily distinguish predefinitive males from females. Rohwer et al. (1980) propose that mimicking plumage but not behavior could still probabilistically fool older males. This process may apply to birds establishing transient breeding territories, but seems unlikely in manakins where males are recruited to pre-existing leks with structured ranks (McDonald 1989; Durães et al. 2008; Ryder et al. 2008b; Cárdenas-Posada et al. 2018).

There are very few reports of predefinitive male manakins siring offspring. The rare records of "stolen" copulations usually still involve definitive males (McDonald 1989; Boyle and Shogren 2019). The only species in which predefinitive males clearly sire young is the Araripe manakin (*Antilophia bokermanni*, Gaiotti et al. 2020), with the possible addition of blue-crowned manakins (Durães et al. 2009). In a study of Araripe manakins, predefinitive males make up 48% of sires, despite not singing or holding territories (Gaiotti et al. 2020). We note that the breeding system of the Araripe manakin is complicated by the fact that the species is critically-endangered, with a small population size and extremely limited range.

Even given these copulations by predefinitive-plumaged males, we lack the data to further differentiate between female-mimicry, juvenile-mimicry, or even crypsis. Indeed, a variation of the crypsis hypothesis could posit that drab predefinitive plumage helps young males hide from territorial males rather than predators. Any study of mimicry in manakin predefinitive plumages must distinguish between mimicry and crypsis (Endler 1981), as well as provide evidence that predefinitive males sire young or gain other resources as a result of successful mimicry.

Status-signaling

The status-signaling hypothesis posits that predefinitive plumages explicitly signal a male's subordinate age, experience, or social status, thereby reducing aggression from older males (Lyon and Montgomerie 1986). More than the other functional hypotheses, status-signaling is supported for the predefinitive plumages of a diverse set of species (Hawkins et al. 2012). Given the structured mating systems of manakins, potential benefits to status-signaling for young males could include opportunities to improve courtship displays through practice and to join the social hierarchies that enable future reproduction. Under this hypothesis, we expect that (1) conspecifics differentiate predefinitive-plumaged males, definitive-plumaged males, and females, (2) young males benefit from being noticed as males, and (3) changes in plumage track changes in social status.

These three predictions are all supported for manakins. First, conspecific males are likely able to differentiate predefinitive-plumaged males from females due to distinct plumages and behavioral cues (see Functional Hypotheses: Mimicry). Anecdotes from round-tailed (*Ceratopipra chloromeros*, Tello 2001) and golden-headed manakins (*Ceratopipra erythrocephala*, Lill 1976) suggest that definitive-plumaged males are less aggressive toward predefinitive-plumaged individuals. More precise observations and experiments from *Chiroxiphia* support these descriptions (Foster 1987; McDonald 1993a). In particular, stuffed models of predefinitive male long-tailed manakins are not attacked by the "alpha" males which obtain copulations via displays, but by other males lower on the local hierarchy (McDonald 1993a). These results are consistent with the idea that predefinitive-plumaged males present a social threat to lower-ranking males but not a reproductive threat to definitive-plumaged breeding males.

Second, predefinitive-plumaged males gain benefits from advertising their sexual and social status. Studies with long-tailed manakins and wire-tailed manakins (*P. filicauda*) show that coalitions with higher-ranking males increase chances of social success and future copulations (McDonald and Potts 1994; McDonald 2007; Ryder et al. 2008b). It further appears that practicing displays can help young males improve their performance for females. In long-tailed manakins, teams of males that practice together develop matching songs and attract more females (Trainer and McDonald 1995; Trainer et al. 2002). In lance-tailed manakins (*C. lanceolata*), "betas" that act as helpers to dominant males do not have a better chance of becoming a copulating alpha male, but first-year alphas with beta experience sire more young than alphas without this experience (DuVal 2013).

Finally, the status-signaling hypothesis is also the only functional hypothesis able to explain both multiple predefinitive plumage stages and intraspecific developmental variation. At least 11 species of manakins have multiple predefinitive plumage stages, in which latter stages include elements distinctly resembling definitive male plumage patches (Table 1). Multiple stages could allow young males to indicate shifts in sexual or social status across multiple years. Further, some individuals delay molt or retain previous plumage stages (e.g., Ryder and Durães 2005), while other rare cases appear to skip across multiple stages (e.g., Doucet et al. 2007a). A facultative link between social context and plumage signaling could explain a halt at a given stage just as much as progress across multiple stages.

Does manakin plumage development dynamically respond to social context? We once again need a better view of the physiological mechanisms enabling development. Research will be complicated by the fact that the link between physiology and sexual signals is not unidirectional. Both plumage and social interactions can provide feedbacks to physiological processes, thus entangling the threads of plumage, behavior, and status (Oliveira 2004; Safran et al. 2008).

The predictions of the status-signaling hypothesis show the closest fit to manakins. However, much of the relevant evidence comes from the genus *Chiroxiphia*. Being accepted within a court may be especially important for reproductive success in this genus, with its complex, cooperative social hierarchies. The benefits of status signaling should be different for species with different social behaviors (Prum 1994a). With ample variation in predefinitive plumages and social systems, the manakin clade is a

unique potential model for future tests of socio-developmental processes.

Conclusion

After reviewing manakin natural history and synthesizing the results of ecological and behavioral studies, we find status-signaling to be the most likely function of manakin predefinitive plumages. Explicit predefinitive signals may help young males gain access to display courts and establish social ties with other males. In contrast, there is nearly no support for the ideas that drab predefinitive plumages help young males effectively hide from predators or mimic females, although direct experiments are needed. Further, no predefinitive plumage patterns can be clearly explained by constrained partial molts, environmental limits in carotenoid pigments, or hormonal ties to reproductive behavior.

We note that the data in this paper were limited to existing descriptions of manakin plumages, and that we used qualitative reasoning to address hypotheses. In addition, our support for the status-signaling hypothesis was largely focused on well-studied *Chiroxiphia* species. Further quantitative studies are needed, especially to assess more general support for status-signaling across manakins. For now, we have sought to demonstrate how a broader understanding of manakin predefinitive plumages speaks to standing hypotheses and raises a variety of research questions in development, physiology, signaling, and macroevolution.

Settling the questions raised here will require a much more detailed knowledge of not only young males, but also the female manakins whose choices establish the evolutionary benefits of definitive plumages and whose plumage evolution establishes the landscape of sexual dichromatism. Here, we echo Odom and Benedict (2018), among others, in the growing call for better attention to the lives of female birds. A great deal of research in ecology and evolution is still waiting for us to expand our focus beyond breeding males.

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Conflict of interest

None declared.

The data underlying this article are available in Table 1.

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