

THAMNOPHILIDAE (ANTBIRD) MOLT STRATEGIES IN A CENTRAL AMAZONIAN RAINFOREST

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ABSTRACT.—Avian molt, or the regularly scheduled replacement of feathers, is an important life history event, particularly in central Amazonian rainforest birds for which a relatively high proportion of the annual cycle can be dedicated to this process. Here, we detail molt strategies of 18 antbird species (Thamnophilidae) based on 2,362 individuals captured from lowland tropical rainforest at the Biological Dynamics of Forest Fragmentation Project near Manaus, Brazil. All species exhibited a molt strategy consistent with the Complex Basic Strategy, in which birds undergo an inserted preformative molt within the first cycle, but apparently lack prealternate molts. The preformative molt and resulting formative plumage aspect of the 18 antbird species can be grouped by three distinct patterns: 1) a complete molt resulting in an adult-like formative plumage without molt limits; 2) a partial molt involving body feathers, lesser coverts, at least some or all median and greater coverts, and sometimes tertials or rectrices, resulting in an adult-like formative plumage with molt limits; and 3) a partial molt as in '2' but resulting in an adult female-like formative plumage in both sexes with plumage maturation delayed in males until the second prebasic molt. In addition, we show that one species, *Percnostola rufifrons*, exhibited an extra inserted molt (a partial auxiliary preformative molt) in the first cycle before initiating a complete preformative molt making this, to our knowledge, the first description of an auxiliary preformative molt for a suboscine. The extent of the preformative molt or delayed plumage maturation was not predicted by ecological guild, raising questions about how phylogenetic relatedness and ecological adaptation drive variation in molt patterns across antbirds. *Received 4 October 2013. Accepted 1 March 2014.*

Key words: auxiliary preformative molt, delayed plumage maturation, molt cycle, preformative molt, understory insectivore.

The durability, aerodynamic capability, and thermoregulatory properties of feathers undoubtedly contributed to the global proliferation of birds. Despite the importance of feather maintenance through regular replacement, or molt, ornithological interest has disproportionately been focused on other phases of the life cycle such as migration and breeding (Bridges 2011). Given that the timing, speed, and extent of molts have cascading effects on the entire avian life cycle, documenting variation in molt strategies among species is a necessary step towards understanding factors that contributed to the evolution of plumage coloration, migration, and courtship behaviors among other aspects of the avian cycle (Humphrey and Parkes 1959; Rohwer et al. 1980, 2005; Svensson and Hederström 1999). In general, molt strategies have been well documented in North American and European taxa (Svensson

1992; Baker 1993; Mulvillhill 1993; Jenni and Winkler 1994; Pyle 1997, 2008; Howell 2010), whereas similar work in the Neotropics is still in its infancy (reviewed in Ryder and Wolfe 2009; see also Ryder and Durães 2005; Guallar et al. 2009; Wolfe et al. 2009a, b; Hernández 2012).

The antbirds (Passeriformes: Thamnophilidae, *sensu* Remsen et al. 2014) are members of a diverse family of suboscines with about 220 species confined to the New World tropics and subtropics (Zimmer and Isler 2003). Antbirds are relatively well studied among Neotropical birds, ranging from the detailed life history descriptions by Willis (1969, 1973), to recent phylogenetic analyses (Brumfield et al. 2007, Moyle et al. 2009, Bravo et al. 2012), to community assembly analyses (Gómez et al. 2010), but their molt strategies have received little attention. From what is known, antbirds apparently follow the Complex Basic Strategy, in which an inserted extra molt, the preformative molt (*sensu* Howell et al. 2003), occurs in the first cycle of a bird's life and ranges in extent among species from partial to complete, although details of the preformative molt in many species have yet to be described (Ryder and Wolfe 2009). Partial molts involve body feathers and some wing coverts, but not flight feathers, resulting in two generations of plumage, and the boundary between retained juvenal and replaced formative

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feathers is referred to as a 'molt limit' (*sensu* Pyle 1997).

Plumage maturation is an important aspect of the preformative molt in many passerines, as this process exchanges a juvenile plumage with a more adult-like plumage. Plumage color is driven by endogenous hormonal signals refined through adaptive necessities or constraints, and the development and deposition of these pigments presumably represent tradeoffs between factors such as energetic cost, social status, and predation risk (Murphy 1996, Hill and McGraw 2006). Delaying plumage maturation until after the formative plumage is a strategy employed by a wide variety, albeit a minority, of temperate and tropical passerines, perhaps most famously among manakins (Pipridae) but also among a variety of other migratory suboscines and oscines (e.g., Thompson 1991, McDonald 1993, Hill 1996, Saetre and Slagsvold 1996). Delayed plumage maturation is often considered an adaptation to a social consequence in which not advertising maturity is adventitious (reviewed in Hawkins et al. 2012). Unfortunately, the frequency and role of delayed plumage maturation within the diverse antbird family has not been systematically examined.

What drives variation in the extent of preformative molts in antbirds? In diverse predominantly temperate passerine families such as Sylviidae, Parulidae or Emberizidae, more extensive preformative molts are common among species living in harsh environments characterized by dense vegetation or increased daily exposure to ultraviolet light. This relationship probably reflects an adaptation in which the juvenile plumage lacks the structural integrity necessary to carry-on day-to-day activities (thermoregulation, flight, etc.) and needs to be quickly replaced by an extensive formative plumage (Dwight 1900, Willoughby 1991, Jenni and Winkler 1994, Pyle 1998, Svennson and Hedenström 1999, Howell 2010, Small et al. 2013). Exposure to ultraviolet light may not be particularly problematic for antbird species that frequent tropical forest understories, with the exception of gap specialists, when compared to migratory temperate species that are exposed to more hours of sunlight throughout the annual cycle. Other factors such as understory vegetation density, distance traveled (ant-following birds commonly travel long distances), and foraging behavior (sallying versus terrestrial insectivores) may exert increased deg-

radation pressures to juvenile feathers and necessitate a more extensive preformative molt extent in antbirds.

In this study, we examine preformative molt variation within a community of rainforest, understory-dwelling antbirds from the central Amazon. More specifically, we describe variation in the preformative molt within and among species, and describe whether this molt results in delayed plumage maturation (i.e., a juvenile or female-like formative plumage in males). After assigning study species to one of four ecological guilds, we discuss whether these guilds are useful predictors of preformative molt characteristics.

METHODS

We captured birds with mist-nets (NEBBA type ATX, 36-mm mesh, 12 × 2 m) from 2007–2012 in continuous and fragmented primary rainforest at the Biological Dynamics of Forest Fragmentation Project (BDFFP), ~80 km north of Manaus, Amazonas, Brazil (2.5° S, 60° W). Mist-nets were placed at ground level in lines of 4, 8, or 16 depending on the site and were open between 0600 and 1400 Amazon Time (AMT) (see Bierregaard et al. 2001 and Stouffer et al. 2006 for details). We sampled primarily during the dry season from June to December; while this may initially appear seasonally limiting for assessing molt strategies, most antbirds at the BDFFP breed and molt in any month of the year (Johnson et al. 2012, Stouffer et al. 2013) providing an opportunity to see all potential age and sex classes and their intermediates during our field season.

There are 28 species of Thamnophilidae known to occur at the BDFFP (Cohn-Haft et al. 1997). We report molt strategies in 18 understory species for which we have adequate samples, excluding three mid-story/canopy species and seven locally rare species (Cohn-Haft et al. 1997, Johnson et al. 2011a). Captured birds were banded and examined for active molt or molt limits, skull ossification, and soft-part colors. When molt limits were suspected, we described the extent of the molt in each feather tract, such as how many greater coverts, rectrices, tertials, primaries, and secondaries were replaced versus retained. Digital images of open wings (e.g., Fig. 1) were also taken to analyze and document molt patterns. Given high capture rates during our banding operations, not all data were recorded from each bird when fast processing was necessary to ensure bird safety.

a) *Pithys albifrons*b) *Percnostola rufifrons*c) *Hypocnemis cantator*d) *Myrmotherula longipennis*

FIG. 1. Representative images of first cycle birds with incompletely ossified skulls, including two species going through complete preformative molts (A, B) and two species with molt limits resulting from a partial preformative molt (C, D). A) *Pithys albifrons*, sex unknown, with p1–2 replaced, p3 growing, p4–10 juvenile; B) *Percnostola rufifrons*, male, with three generations of feathers including juvenile (five outer greater coverts, primary coverts, secondaries, and primaries), female-like auxiliary formative (lesser and median coverts), and adult-male-like formative (four median coverts and two greater coverts); C) *Hypocnemis cantator*, male, with molt limits among the greater coverts (the outer five greater coverts, carpal covert, primary coverts, secondaries, and primaries are retained from the juvenile plumage); D) *Myrmotherula longipennis*, sex unknown, with molt limits among the greater coverts (the inner four are replaced/formative and the outer five are retained/juvenile; the carpal covert, primaries and secondaries are also retained from the juvenile plumage).

We assessed the extent of preformative molts using two criteria. First, we looked for clear evidence of mixed juvenile and adult-like (i.e., formative) feathers in all birds whether molting or not. Juvenile feathers in Thamnophilidae are distinct from subsequent plumages by having loosely textured feathers with lower barb densities than in subsequent plumages, having distinct coloration, and having distinct shapes with rectrices being more pointed and longer, greater coverts being shorter, and remiges being shorter (Dwight 1900, Zimmer and Isler 2003). Second, we looked for molt limits in birds that were not molting that appeared consistent in extent among other individuals of the same species. We follow

Pyle (1997) and define a molt limit as an interruption in a molt episode that is arrested, i.e., the molt does not continue later but starts over at the next episode. We recorded details of the numbers of feathers replaced in relevant feather tracts, including the greater coverts, secondaries, primaries, primary coverts, and rectrices, as well as the presence or absence of molt limits among median coverts. For sexually dichromatic species (i.e., all species with the exception of *Pithys albifrons*), we also noted whether the resulting formative plumage aspect was adult-female-like or adult-male-like.

We also evaluated other criteria for aging birds, which was helpful to assign observations of active

molt or molt limits into age brackets. First, we looked for changes in soft-part colors, such as in the iris, bill, or tarsus, and determined when particular species reached an adult-like color relative to the molt status. Second, we examined skulls for ossification, which often completes in passerines between six and eight months of age, before the second prebasic molt initiates (Nero 1951, Pyle 1997). To our knowledge, no detailed account of skull ossification timing exists for antbirds, but ossification is believed to complete or nearly complete in a similar timeframe as found in other passerines (Capparella et al. 1997, Isler et al. 1997, Tallman and Tallman 1997, Zimmer and Isler 2003).

We categorized each species into an ecological guild that represents foraging strategy and habitat use, following Stouffer et al. (1995). These guilds included obligate mixed-species flock members, gap or disturbed-forest specialists, obligate ant-followers, and other understory insectivores (Table 1).

RESULTS

We accumulated 3,859 captures representing 2,764 individual antbirds after 48,898 mist-net hours of effort, ultimately aging 2,362 individuals (85.5%; Appendix A). We found that all 18 study species followed a Complex Basic Strategy. Preformative molts grouped into three distinct patterns (Table 1): 1) complete, resulting in an adult-like formative plumage (Fig. 1a, b); 2) partial, with replaced adult-like body feathers, lesser coverts, at least some or all median and greater coverts, and sometimes tertials or rectrices in both sexes (Fig. 1c); and 3) partial, as in '2' but always resulting in an adult female-like formative plumage in both sexes with plumage maturation delayed in males until the second prebasic molt (Fig. 1d). In species with complete preformative molts, the skull always ossified during the preformative molt, sometime between the replacement of primary 1 and 6 (Fig. 2, Table 2), whereas in species with partial preformative molts, i.e., not involving flight feather replacement, the skull ossified after the completion of the preformative molt (Table 2).

Five of 18 study species showed a complete preformative molt (Table 1). In these species, the resulting formative plumage was essentially identical to subsequent definitive basic plumages (i.e., 'adult'-like). One species, *P. albifrons*, was sexually monochromatic and the other four were sexually dichromatic in the formative and defin-

itive basic plumages. We concluded that these complete post-juvenile molts were consistent with a preformative molt (*sensu* Howell et al. 2003) using four criteria. First, continuous body and wing molt always followed a distinct juvenile plumage. Second, an interrupted molt that was consistent with a partial or incomplete molt was not observed or predominant in these species. Third, soft-part colors, such as iris color (in *Gymnopathys rufigula*, *Frederickena viridis*, *Thamnophilus punctatus*, and *Percnostola rufifrons*) and tarsus color (in *P. albifrons*) transitioned into an adult-like coloration before completion of the post-juvenile molt. Finally, we examined the timing of skull ossification in *P. albifrons*, *G. rufigula*, and *P. rufifrons* and found that it completed between the replacement of primary 1 and 6 (Table 2, Fig. 2).

The remaining 13 study species showed molt limits resulting from a partial preformative molt (Table 1). Multiple individuals of these species showed similar molt limits among the median coverts, greater coverts, tertials, and/or rectrices, and there was no evidence for more extensive or complete preformative molts in these species (Table 2). In some species (e.g., *Thamnomanes caesius*), more feathers were replaced in the median and greater coverts, on average, than in other species (e.g., *Epinecrophylla gutturalis*). Similarly the frequency and extent of tertial and rectrix replacement was greater in some species, particularly those that replaced more greater coverts (Table 2). In five of these species, we were able to recapture at least one individual that retained the identical molt limit for at least 15 days and up to 186 days later (Appendix B), confirming that molt limits were not the result of actively molting birds or molt suspensions. In all species, we found that the skull had completely ossified before the second prebasic molt initiated, and in seven species we found individuals with molt limits with either ossified or incompletely ossified skulls, suggesting the skull ossified during or shortly after completion of the preformative molt (Table 1).

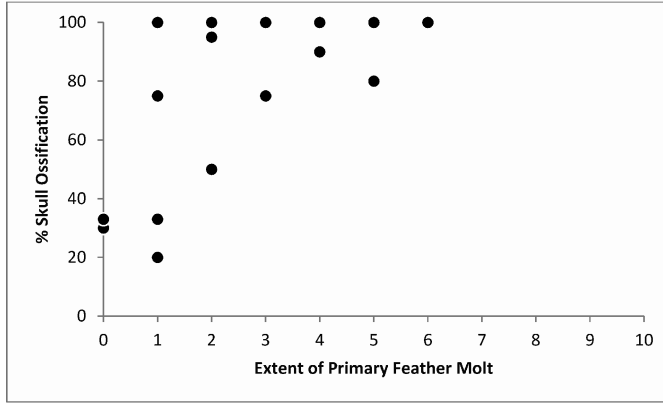
In all 13 species with partial preformative molts, the second (definitive) basic plumage was sexually dichromatic, but in only nine of these were replaced formative plumage feathers in both sexes similar to subsequent definitive basic counterparts. The remaining four species exhibited delayed plumage maturation in males with the formative plumage appearing adult female-like;

TABLE 1. The percentage of individuals with unossified skulls (and number of individuals examined) in each age category (following Wolfe et al. 2010, Johnson et al. 2011b) indicating the timing of skull ossification. In all species (with one exception^a), the skull ossifies before the initiation of the SPB/DPB, i.e., during the FCF in species with partial preformative molts and during the FPF in species with complete preformative molts (see also Fig. 2). Also indicated is the ecological guild for each species (A = understory insectivore; B = gap or disturbed-forest species; C = ant-follower; D = obligate mixed-flock member).

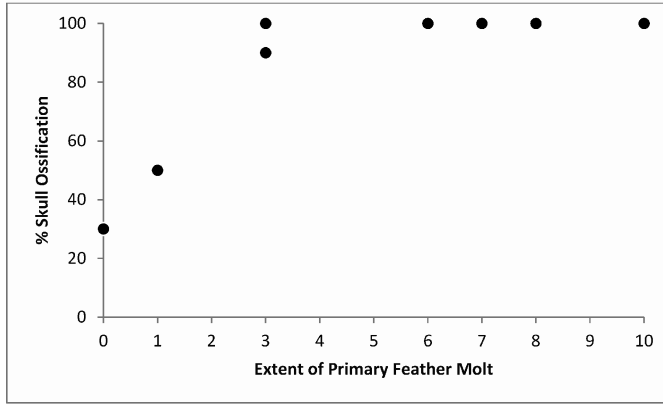
Species	Guild	Age Category						
		FPI or FCI	FPF	FCF	FAJ	SPB	DCB	DPB
Complete preformative molt								
<i>Frederickena viridis</i>	A	-	-		0.0 (11)			-
<i>Thamophilus punctatus</i>	B	-	-		0.0 (1)			-
<i>Percnostola rufifrons</i>	B	-	31.6 (19)		0.0 (12)			0.0 (9)
<i>Ptilys albigrons</i>	C	100.0 (11)	51.3 (39)		1.8 ^a (56)			0.0 (11)
<i>Gymnophrys rufigula</i>	C	100.0 (5)	36.4 (11)		0.0 (29)			0.0 (5)
Partial preformative molt – sexually dichromatic								
<i>Thamophilus murinus</i>	B	-	-	20.0 (5)				0.0 (1)
<i>Thamomanes ardesiacus</i>	D	-	100.0 (1)	20.0 (10)				0.0 (2)
<i>Thamomanes caesiatus</i>	D	-	-	4.8 (21)				0.0 (3)
<i>Isleria guttata</i>	A	-	-	-				0.0 (2)
<i>Epinecrophylla gutturalis</i>	D	100.0 (1)	-	81.3 (16)				0.0 (1)
<i>Myiotherula axillaris</i>	B	-	-	0.0 (9)				0.0 (1)
<i>Hypocnemis cantator</i>	B	-	100.0 (1)	11.1 (9)				0.0 (1)
<i>Myrmeciza ferruginea</i>	A	-	100.0 (3)	-				0.0 (2)
<i>Hylotylax naevia</i>	A	-	-	-				0.0 (2)
Partial preformative molt – delayed plumage maturation								
<i>Myiotherula longipennis</i>	D	-	-	0.0 (6)				0.0 (3)
<i>Myiotherula menetriesii</i>	D	-	-	100.0 (2)				0.0 (6)
<i>Schistochila leucostigma</i>	B	100.0 (1)	100.0 (1)	66.7 (3)				0.0 (3)
<i>Willisornis poecilinota</i>	A	-	100.0 (1)	23.5 (17)				0.0 (10)

^a Skull was estimated to be 90% ossified in one individual.

a) *Pithys albifrons* (n = 26)



b) *Gymnopathys rufigula* (n = 11)



c) *Percnostola rufifrons* (n = 23)

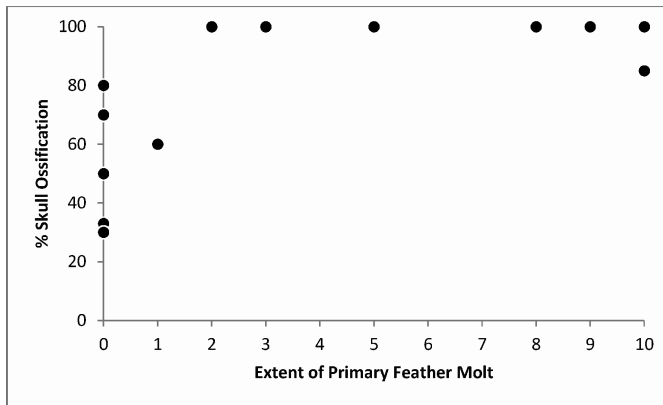


FIG. 2. The relationship between ossification and feather molt of primaries in three species with complete preformative molts: a) *Pithys albifrons*; b) *Gymnopathys rufigula*; c) *Percnostola rufifrons*.

TABLE 2. The number of replaced feathers (range, median, and absolute median deviation [MAD]) in four different feather tracts during partial preformative molts and the number of individuals examined (n) for 13 species of Thamnophilidae.

Species	Median coverts:			Greater coverts:			Tertials:			Rectrices:		
	% with limits (n)	Range (n)	Median ± MAD	Range (n)	Median ± MAD	Range (n)	Range (n)	Median ± MAD	Range (n)	Median ± MAD	Range (n)	Median ± MAD
<i>Thamnophilus murinus</i>	0.0 (2)	2-9 (3)	3 ± 1	0 (2)	0 ± 0	0 (2)	0 (1)	0 ± 0	0 (1)	0 ± 0	0 (1)	0 ± 0
<i>Thamnomanes ardesiacus</i>	9.1 (11)	1-9 (22)	6 ± 3	0-2 (15)	1 ± 0	0-2 (15)	0 (3)	1 ± 0	0 (3)	0 ± 0	0 (3)	0 ± 0
<i>Thamnomanes caesius</i>	40.0 (15)	0-9 (34)	6 ± 2	0-3 (20)	2 ± 1	0-3 (20)	0-6 (9)	2 ± 1	0 (2)	0 ± 0	0 (2)	0 ± 0
<i>Isleria guttata</i>	100.0 (1)	5 (1)	5 ± 0	2 (1)	2 ± 0	2 (1)	0 (1)	2 ± 0	0 (1)	0 ± 0	0 (1)	0 ± 0
<i>Epinecrophylia gutturalis</i>	37.5 (16)	0-8 (19)	0 ± 0	0 (16)	0 ± 0	0 (16)	0 (4)	0 ± 0	0 (4)	0 ± 0	0 (4)	0 ± 0
<i>Myrmotherula axillaris</i>	0.0 (12)	1-9 (17)	4 ± 2	0-3 (13)	0 ± 0	0-3 (13)	0 (4)	0 ± 0	0 (4)	0 ± 0	0 (4)	0 ± 0
<i>Myrmotherula longipennis</i>	0.0 (2)	1-9 (5)	3 ± 2	0-1 (4)	0 ± 0	0-1 (4)	0 (3)	0 ± 0	0 (3)	0 ± 0	0 (3)	0 ± 0
<i>Myrmotherula menetriesii</i>	0.0 (1)	3 (1)	3 ± 0	0 (1)	0 ± 0	0 (1)	-	0 ± 0	-	0 ± 0	-	0 ± 0
<i>Hypocnemis cantator</i>	8.3 (12)	0-8 (17)	3 ± 2	0-1 (14)	0 ± 0	0-1 (14)	0 (7)	0 ± 0	0 (7)	0 ± 0	0 (7)	0 ± 0
<i>Schistocichla leucostigma</i>	0.0 (3)	1-6 (4)	4 ± 1	0 (3)	0 ± 0	0 (3)	0 (2)	0 ± 0	0 (2)	0 ± 0	0 (2)	0 ± 0
<i>Myrmeciza ferruginea</i>	0.0 (5)	8-9 (5)	8 ± 0	0 (5)	0 ± 0	0 (5)	0 (3)	0 ± 0	0 (3)	0 ± 0	0 (3)	0 ± 0
<i>Hylophylax naevia</i>	100.0 (1)	1-5 (2)	3 ± 2	0 (1)	0 ± 0	0 (1)	-	0 ± 0	-	0 ± 0	-	0 ± 0
<i>Willisornis poecilinota</i>	0.0 (8)	0-9 (23)	3 ± 1	0-3 (9)	0 ± 0	0-3 (9)	0 (6)	0 ± 0	0 (6)	0 ± 0	0 (6)	0 ± 0

the adult male plumage aspect was not acquired until the second prebasic molt.

In one species, *P. rufifrons*, an apparent extra, or third, molt in its first cycle was noted, which we call an auxiliary preformative molt following Howell et al. (2003), also referred to as a presupplemental molt by Rohwer (1986), Thompson (1991), and Pyle (1997). In this species, this partial molt replaced juvenile body, lesser coverts and some median coverts with adult female-like feathers in both sexes, and was quickly followed by a sexually dichromatic complete preformative molt that initiated before the skull ossified (Fig. 2c, Table 1). Therefore, three generations of feathers were apparent on birds early in the preformative molt, which was particularly obvious in males (Fig. 1b). The skull ossified before this complete molt concluded, similar to other antbird species with complete preformative molts (Fig. 2, Table 1).

Preformative molt strategies were not apparently associated with ecological guild as all three preformative molt strategies were utilized by multiple ecological guilds (Table 1). Each of the three preformative molt strategies was observed in three of four guilds. Only the obligate ant-follower guild aligned with one preformative molt strategy, but there were only two species to consider in this guild.

DISCUSSION

All 18 species of antbird that we examined appeared to follow a molt strategy that was consistent with the Complex Basic Strategy and preformative molts were variable in extent across species, as indicated by Ryder and Wolfe (2009). Although we could not conclusively eliminate the possibility of an undetected prealternate molt in this study, it seems unlikely that prealternate molts exist in these species, as few other resident tropical forest species apparently exhibit prealternate molts (Howell et al. 2003, Ryder and Wolfe 2009). Complete wing molts in these antbirds can take 155 days (*M. menetriesii*) to 301 days (*P. albifrons*), leaving little time in an annual cycle to insert additional molts, although molt cycles may not be annual in some ant-followers (e.g., *P. albifrons*, J. Chaves-Campos, pers. comm., Johnson et al. 2012), and prealternate molts have a potential to overlap protracted preformative or definitive prebasic molts. Because individuals of antbirds at the BDFFP can molt or breed at any time year (Johnson et al. 2012, Stouffer et al.

2013), distinguishing body molts from other scheduled molts and adventitious feather replacement would require an in-depth examination of body feather tracts using recaptured birds. Our data indicate that partial prealternate molts involving wing coverts or tertials, at least, do not occur.

To our knowledge, *P. rufifrons* is the first suboscine described to have an auxiliary preformative molt inserted between the juvenile and formative plumages in the first cycle. An alternative explanation for what we call the auxiliary preformative molt (*sensu* Howell et al. 2003) in *P. rufifrons* is that this is instead a partial preformative molt that results in a female-like plumage, which is then followed by a complete second (definitive) prebasic molt, a strategy exhibited by *Myrmotherula longipennis*, *Myrmotherula menetriesi*, *Willisornis poecilinota*, and *Schistocichla leucostigma*. In this scenario, the second prebasic molt would begin while the skull is incompletely ossified (Fig. 2c), suggesting an advancement of the second prebasic molt by at least six months. This idea was also posed as an alternative for explaining Ruby-throated Hummingbird molts (P. Pyle, in Cardiff and Dittmann 2009), and such a dramatic temporal advancement of the second prebasic molt would represent a novel strategy for molt in birds. We instead suggest that this inserted partial first-cycle molt in *P. rufifrons* is indeed an auxiliary preformative molt and that the subsequent complete molt is a preformative molt, based on consistencies with complete preformative molts in other antbirds. First, the skull ossified during the complete molt, consistent with the other species that exhibited a complete preformative molt. Second, the iris transitioned from a juvenile brown color to an adult red (in males) or orange (in females) color during this complete molt, comparable to soft-part transitions in other antbird species with complete preformative molts. Third, the plumage resulting from the partial molt was never observed for more than a few weeks before it began transitioning into the next complete molt, unlike the plumages resulting from partial preformative molts that often lasted months in other species.

It was perhaps surprising that four of our 18 study species showed delayed plumage maturation, a phenomenon not well-documented in Thamnophilidae (Zimmer and Isler 2003). A number of hypotheses have been proposed to explain delayed plumage maturation in other

birds, particularly for independent subadults of temperate migratory species (reviewed in Thompson 1991) and lekking species (Foster 1987, McDonald 1993, Anciães and Del Lama 2002, Ryder and Durães 2005). These hypotheses are founded on explanations related to the social environment (Hawkins et al. 2012), such as the juvenile mimicry hypothesis (Lawton and Lawton 1986, Foster 1987) and summer female mimicry hypothesis (Rohwer et al. 1980), but slight modifications to these hypotheses may be necessary when considering non-lekking resident tropical species. Our antbird study species maintain year-round territories held by an often sexually monogamous male-female pair, thus breeding is expected to be reserved for territory-holding individuals (Stutchbury and Morton 2001, Zimmer and Isler 2003).

In non-lekking resident Neotropical species with delayed plumage maturation, we hypothesize that delayed plumage maturation may correlate with delayed natal dispersal. Interestingly, we have observed brood patches during the formative plumage in several species that do not undergo delayed plumage maturation, such as *Thamnomanes* and *E. gutturalis*, suggesting they disperse from their natal territory and at least attempt to breed in territories of their own within their first cycle of life. To the contrary, in all four species that show delayed adult male plumage acquisition, we have not observed brood patches in formative-plumaged birds. From these observations, we postulate that the acquisition of adult-like male feathers during the preformative molt may be linked to hormonal signals that facilitate breeding in the first cycle, and certainly further study is needed to corroborate this. Non-exclusive mechanisms related to delayed natal dispersal and delayed plumage maturation in antbirds may include assisting with rearing offspring (as in some Australian fairy-wrens; Schodde 1982), remaining on natal territories to increase lifetime fitness and fecundity, or life-history traits resulting in breeding territory saturation. The hypothesized relationship between delayed breeding or territory acquisition and delayed plumage maturation should be tested with data on the timing of natal dispersal relative to the preformative molt in antbirds, along with an exploration of mechanisms that may help drive these patterns.

Molt strategies may be adaptive and optimized in response to drivers that include environmental conditions, migration strategy, and social require-

ments (Rohwer et al. 2009, Howell 2010). Here, we show substantial variation in preformative molt strategies of non-migratory birds occurring in similar habitats, from a single location, and within a single taxonomic family. The observed variation in molt presents an interesting opportunity to relate these strategies to other life history traits, relatively independent of environmental conditions; however, preformative molt strategies did not align with our classifications of ecological guilds with three of four guilds represented in each of three preformative molt strategies. It may be that ecological guilds *per se* are less important than explicit measures of the density of vegetation and exposure to ultraviolet light – unfortunately measurements of these environmental conditions in occupied habitat-space do not exist for these species. As an exception, complete preformative molts were found in both species of ant-followers, an ecological category confounded with taxonomic relatedness as all obligate ant-following antbirds cluster within the Pithyini Tribe (Brumfield et al. 2007, Moyle et al. 2009). A complete preformative molt resulting in an “adult-like” plumage has also been described in other ant-followers including *Rhegmatorhina gymnops* (Willis 1969) and *Phaenostictus mcleannani* (Willis 1973), suggesting complete preformative molts are wide-spread and shared among ant-followers, posing the question whether complete preformative molts among obligate ant-followers is a result of phylogenetic inertia, convergence on optimized strategy for ant-following, some other factor, or all of the above.

Although we assessed molts in fewer than 10% of the *Thamnophilidae* species, our results suggest that preformative molt patterns may not necessarily be phylogenetically conserved, with perhaps the exception of ant-followers (Brumfield et al. 2007, Moyle et al. 2009). For example, in two species of *Thamnophilus*, one showed a complete preformative molt whereas the other showed a partial preformative molt. In the five ‘antwren’ species (*Myrmotherula*, *Iseria*, and *Epinecrophylla*), all showed partial preformative molts but with different levels of plumage aspect maturation. Among the closely-related *Pernostola*, *Schistocichla*, and *Myrmeciza*, respective preformative molts were complete, partial with delayed plumage maturation in males, and partial and sexually dichromatic.

Only once molt and plumage strategies are described in other antbirds, can advances in understanding their population biology be realized, which

is particularly critical as these Neotropical species face increased habitat alteration in the coming decades. This large and ecologically diverse family may also be a particularly interesting model for examining functional and evolutionary mechanisms that drive variation in molt strategies across species. Revealing these patterns might help elucidate adaptive responses to social, ecological, and evolutionary forces and lead to a more comprehensive understanding of avian life histories.

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APPENDIX A. The number of individuals in each age category captured/recaptured near Manaus, Brazil for 18 species of Thamnophilidae grouped by preformative molt strategy. FPJ = first prejuvenile molt; FCJ = first cycle juvenile plumage; FPF = first preformative molt; FCF = first cycle formative plumage; SPB = second prebasic molt; DCB = definitive cycle basic plumage; DPB = definitive prebasic molt; FAJ = after juvenile plumage (age codes follow Wolfe et al. 2010, Johnson et al. 2011b).

Species	FPJ or FCJ	FPF	FCF	SPB	DCB	DPB	FAJ
Partial preformative molts – sexually dichromatic							
<i>Thamnophilus murinus</i>	0/0	1/0	8/0	4/1	34/5	10/1	-
<i>Thamnomanes ardesiacus</i>	7/0	4/0	33/3	39/5	120/26	34/5	-
<i>Thamnomanes caesius</i>	6/0	5/0	68/2	35/4	94/21	28/1	-
<i>Isleria guttata</i>	0/0	0/0	1/0	2/0	1/0	3/1	-
<i>Epinecrophylla gutturalis</i>	4/0	2/0	27/1	4/0	62/6	20/4	-
<i>Myrmotherula axillaris</i>	0/0	2/0	32/4	17/1	51/7	18/3	-
<i>Hypocnemis cantator</i>	3/0	3/0	31/2	13/0	82/17	22/1	-
<i>Myrmeciza ferruginea</i>	2/0	4/0	9/0	1/0	23/6	15/2	-
<i>Hylophylax naevia</i>	1/0	0/0	2/0	0/0	3/0	0/0	-
Partial preformative molts – delayed plumage maturation							
<i>Myrmotherula longipennis</i>	2/0	2/0	15/0	20/3	77/12	26/2	-
<i>Myrmotherula menetriesii</i>	0/0	0/0	5/0	12/3	40/2	7/0	-
<i>Schistocichla leucostigma</i>	1/0	1/0	6/0	4/0	14/1	4/0	-
<i>Willisornis poecilinota</i>	2/0	3/0	63/11	38/11	156/37	82/24	-
Complete preformative molts							
<i>Frederickena viridis</i>	0/0	3/0	-	-	-	3/0	18/3
<i>Thamnophilus punctatus</i>	0/0	1/1	-	-	-	0/0	2/0
<i>Percnostola rufifrons</i>	2/0	57/7	-	-	-	53/10	87/18
<i>Pithys albifrons</i>	93/8	211/38	-	-	-	168/26	218/41
<i>Gymnopithys rufigula</i>	14/0	25/1	-	-	-	20/2	123/26

APPENDIX B. Individuals with molt limits (indicating formative plumage) recaptured at least 15 days later with identical molt limits near Manaus, Brazil.

Species	Individual	Days between captures
<i>Thamnomanes caesius</i>	E34895	49
	E44087	18
<i>Epinecrophylla gutturalis</i>	D95268	128
<i>Myrmotherula axillaris</i>	E49364	186
	C43752	40
	C38335	28
<i>Hypocnemis cantator</i>	C38336	28
	4H6455	181
	D93777	42
<i>Willisornis poecilinota</i>	E44116	119
	E43839	40
	E79385	33
	E128621	24
	E44082	18
	E44123	16

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