ORNITOLOGÍA NEOTROPICAL
SPECIAL ISSUE (2018) 29: S63–S73

ORIGINAL ARTICLE

Sociedad de Ornitología Neotropical

MOLT PATTERNS AND SEXING AND AGING CRITERIA FOR TEN SPECIES OF HIGH ELEVATION LANDBIRDS FROM SOUTHEASTERN PERU

Jeremiah J. Kennedy[1] · Julian Heavyside[2] · Jill E. Jankowski[2] · Micah N. Scholer[2]

[1] CW 405 Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

[2] Biodiversity Research Centre and Department of Zoology, University of British Columbia, 4200 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

E-mail: Jeremiah J. Kennedy · jckennedy@ualberta.ca

Abstract · Knowledge of molt patterns and their resulting plumages is useful for aging and sexing birds and, in monochromatic species, morphometric measurements can help to discern males from females. However, these data are largely undescribed for the majority of the world's bird species, especially in the tropics. We sought to classify the molt strategy for 10 species of Neotropical passerines during their breeding seasons and considered whether a combination of wing chord, tail length and mass could be used to determine their sex. We used banding data from three years of mark-recapture study at Wayqecha Biological Station (2900 m a.s.l.) along the east slope of the Andes in southeastern Peru to characterize molt and estimate morphological measurements. Each of the species exhibited a complete definitive prebasic molt and either a partial (nine species) or partial-incomplete (one species) preformative molt, which we interpreted to be consistent with a complex basic molt strategy. For five of the 10 species, we found that wing, tail, and body mass measurements were useful in distinguishing between males and females. This study contributes to our understanding of tropical bird molt by providing previously undescribed aging and sexing criteria for some tropical landbirds common to high elevations of southern Peru.

Resumen · Patrones de muda y criterios para categorizar sexo y edad en diez especies de aves altoandinas en el sureste de Perú

Los patrones de muda en la mayoría de las aves Neotropicales son poco conocidos y en especial se desconoce si las medidas corporales pueden ser usadas para determinar el sexo en especies sin dimorfismo sexual. En este trabajo clasificamos la estrategia de muda para 10 especies de paserinos Neotropicales y también exploramos si una combinación de medidas de longitud del ala, longitud de la cola y masa corporal pueden ser usadas para la determinación del sexo. Usamos datos de anillamiento de tres años de un estudio de recaptura en la Estación Biológica Wayqecha (2900 m s.n.m.) en el flanco oriental de los Andes al sureste de Perú. Cada especie exhibió una estrategia básica compleja de muda con una muda prebásica definitiva compleja, y una muda preformativa parcial (nueve especies) o parcial-incompleta (uno especie). Para cinco de cada 10 especies, la combinación de medidas de la longitud del ala, la cola, y la masa corporal sirvieron para distinguir entre machos y hembras. Este estudio contribuye a la creciente literatura sobre los patrones de muda en aves tropicales y provee herramientas para clasificar la edad y el sexo de aves con plumaje sexualmente monocromático.

Key words: Andean cloud forest · Definitive basic plumage · Formative plumage · Manu National Park · Molt cycle · Parulidae · Passerellidae · Preformative molt · Thraupidae · Troglodytidae · Tyrannidae

INTRODUCTION

An understanding of avian plumage and molt cycles enables placement of birds into standardized age and sex classes. Distinguishing between these classes is important as behavior and fitness outcomes can vary across different life history stages, such as breeding vs non-breeding (Pagen et al. 2000, Sillett & Holmes 2002), juvenile vs adult (Figuerola et al. 2001, Vitz & Rodewald 2006, Tarwater et al. 2011, Cox et al. 2014), and male vs female (Morton 1990, Sillett & Holmes 2002). Although advanced in Europe (Jenni & Winkler 1994) and temperate North America (Pyle 1997), the study of molt cycles and resultant plumages in other parts of the world remains largely unexplored. Recently, however, the ever-growing interest on the subject has resulted in molt and plum-

Receipt 26 December 2017 · First decision 8 January 2018 · Acceptance 23 May 2018 · Online publication 8 June 2018

Communicated by Rafael Rueda-Hernández, Angelina Ruiz-Sánchez, Santiago Guallar, Peter Pyle

age descriptions of several hundred, mostly Neotropical, landbirds (Pyle et al. 2004, Guallar et al. 2009; Wolfe et al. 2009a, 2009b; Radley et al. 2011, Hernández 2012, Johnson & Wolfe 2014, Guallar et al. 2016, Pyle et al. 2016, Johnson & Wolfe 2017, Tórrez & Arendt 2017). Nonetheless, molt patterns in most Neotropical birds remain undescribed. We studied plumages and molt patterns of birds of southeastern Peru to further our understanding of avifaunal molt in the tropics. Here we summarize our findings for 10 Neotropical passerines common to high elevation cloud forests in the Peruvian Andes and describe their preformative and definitive basic molts and resulting plumages.

METHODS

We conducted our study in the buffer zone of Manu National Park, Peru, at Wayqecha Biological Station (13°11′14.4′′S, 71°35′9.3′′W, 2900 m a.s.l.). Wayqecha is located at the upper extent of montane cloud forest and contains several distinct habitat types including primary growth montane forest, montane scrub, and *Chusquea* sp. bamboo patches below and puna grassland above the treeline (> 3100 m a.s.l.; Jankowski et al. 2013). The high elevation results in relatively stable and cool mean annual temperature of 11.8°C and mean annual rainfall of 1560 mm (Girardin et al. 2014), punctuated by a distinct rainy season beginning in November and extending through April.

Ten survey sites located along 8.5 km of single-track trail were sampled between 2014–2016 as part of a long-term population monitoring project (MNS unpubl. data). Each site consisted of an array of 10–15 mist-nets (12 x 3 m, 36 mm mesh) spaced 5–50m apart. We visited sites for two consecutive days from ca. 06:00–16:00 h. During 2014 and 2015 a repeat visit was made to each site 7–14 days after initial sampling for a total of four days of mist-net surveys, while only a single two-day sampling bout occurred in 2016 (i.e., 10 days of mist-netting at each of the 10 sites). We timed data collection to overlap with the end of the dry season (September–November), which also marks the initiation of breeding for most birds in the region (Terborgh et al. 1990, Hosner et al. 2015).

We selected 10 species for analysis based on the total number of individuals captured and the proportion of those birds that were later recaptured (minimum number of individuals per species = 11, mean ratio of captures/recaptures = 0.46 ± 0.02). We marked each bird with a privately issued aluminum leg band (National Band and Tag, Newport, KY), took standard morphometric measurements (i.e., natural wing chord, length of tail to the end of the longest rectrix, bill length from nares to tip, culmen width measured at the anterior edge of the nares, and body mass) following Pyle (1997), and documented the presence and location of molt limits. We also recorded the extent of active and completed molt for approximately 75% of captured individuals with the goal of describing the range of feathers replaced within each feather tract (e.g., median coverts, greater coverts, etc.); information on the remaining 25% was not recorded if, for instance, birds escaped during processing, were released early because of safety concerns (i.e., onset of rain and inclement weather, birds exhibiting symptoms of stress), or because of observer uncertainty regarding the number of retained and replaced feathers. Importantly, because our study was conducted as part of a long-term monitoring project to estimate apparent annual survival of tropical birds (MNS unpubl. data), we were able to confirm the presence of age-specific molt and plumage patterns by observing recaptured birds across multiple years, among, and within seasons.

When referring to a feather's relative position along the wing we used inner and outer in place of proximal and distal, respectively. We followed Pyle (1997) in describing molt extents; "flight feathers" refer to the rectrices and remiges and include the primary coverts. A "limited" molt extent refers to when flight feathers and some, but not all body feathers are replaced. "Partial" refers to when some to all the body feathers, but no flight feathers are replaced. Partial molts can also include few to all tertials and a pair of central rectrices. "Incomplete" indicates that most to all body feathers, and at least some flight feathers, excluding the tertials, or all rectrices have been replaced and "complete" refers to when all feathers are replaced (Pyle 1997). Molt and plumage terminology follows that of Humphrey and Parkes (1959) as revised by Howell et al. (2003). We refer to the first molt following juvenile plumage as the preformative molt, which results in formative plumage. In most passerines, the annual prebasic molt, which includes the prejuvenile molt (i.e., first prebasic molt) as well as subsequent annual prebasic molts, is complete and these molts and molt cycles are referred to as definitive. As we focused our study over only one part of the annual cycle (i.e., the breeding season) our main goal was to describe the preformative molt and formative plumage of each species. We also describe the definitive basic plumage and note that prealternate molts may also occur in some of these species outside of our sampling period.

For sex specific morphometric measurements, we determined sex when possible based on the presence of a brood patch in females and cloacal protuberance in males. No males of the species we studied are known to assist in incubation or brooding young and therefore do not develop brood patches. We tested for differences between wing chord, tail length, and mass in males and females using a Student's *t*-test in R (R Development Core Team 2017) with *p*-values adjusted for experimental-wise error rates using a Bonferroni correction (Zar 1996). Only species with > 5 individuals represented by each sex were included in the sex-specific morphometric analysis.

RESULTS

We described molt patterns and aging criteria for 10 resident species common to high Andean cloud forests of southeastern Peru. For all the species we studied, presence of molt limits within the greater coverts or between greater and primary coverts (Figure 1) facilitated separation of formative- and definitive-plumage individuals. Sample sizes and morphological measurements for all species are summarized in Table 1. For five of these species, we found select measurements to be useful in distinguishing between sexes with wing chord being the most common criteria for separating males from females (Table 2). Each species appeared to undergo a complete definitive prebasic molt with one species suspending or arresting definitive prebasic molt in a portion (< 10%) of the population. Most (nine species) exhibited a partial preformative molt.

Streak-necked Flycatcher (*Mionectes striaticollis*). The preformative molt generally included all lesser, median, and greater coverts, but no tertials, primary coverts, or rectrices. Juvenile, formative and definitive basic plumages appeared similar, but birds in their first basic plumage had a greenish wash to the nape and crown and limited to indistinct streaking in the throat and breast. In addition, median and greater coverts had more extensive ochraceous tipping and the back and rump feathers were dull yellow-green compared with the more vibrant formative and definitive basic plumages.

The formative plumage was identified by contrasts between both the color and shape of the median and greater coverts. Primary coverts were relatively narrow and pointed with little green edging and greater coverts were relatively broad with more extensive and brighter green edging. In four individuals (14% of cases), only the innermost two or three greater coverts were replaced resulting in a contrast between the fresh, broad and bright-green edged replaced inner greater coverts and the relatively worn, narrow, and yellow-green edged retained outer greater coverts. Retained rectrices were narrow and pointed with a brownish wash; one of the more helpful clues for separating age classes in this species. Primary nine was not notched in formative-plumage females, whereas formative-plumage males sometimes had a slight notch.

The definitive basic plumage had relatively broad and fresh primary coverts and rectrices. All coverts and tail feathers had bright green edging with no brownish wash. As in Olive-striped Flycatcher (*Mionectes olivaceus*) (Wolfe et al. 2009a), the ninth primary was deeply notched along much of the feather in males and slightly notched at the distal end in females (Figure 2). Eleven (10%) of the definitive-plumage individuals captured, specifically females, retained a symmetrical block of two to six inner secondaries. When three or more secondaries were retained, a symmetrical block of one to four outer primaries were also retained; consistent with an incomplete definitive prebasic molt following a typical replacement sequence. All three morphological measurements were statistically different between sexes with males having on average 10% larger wings and tails and 16% greater mass than females (Table 2).

Fulvous Wren (*Cinnycerthia fulva*). The preformative molt ranged from partial to incomplete with zero to three inner primaries, tertials, and rectrices replaced. Juvenile plumage was more reddish-brown above with a lighter cream-colored throat, belly, and superciliary. The lower mandible was orange and the iris gray in color.

The preformative molt included replacement of two to eight inner greater coverts, which had indistinct barring that contrasted with the rufous-washed and boldly-barred juvenile coverts. Unlike temperate North American wrens (Pyle 1997), some Fulvous Wrens (4 of 15 formative-plumage birds captured) had undergone an incomplete preformative molt that followed a typical replacement sequence rather than an eccentric pattern. The replaced remiges were darker in color and had denser barring (Figure 3). These same individuals also replaced one to two inner rectrices that showed a similar pattern of coloration and barring to those of replaced remiges. Formative-plumage individuals could also be separated from definitive-plumage individuals by a brownish iris and generally more worn appearance during the breeding season.

The definitive basic plumage had uniformly brown greater coverts with barring that formed a gradient from indistinct on the inner, to distinct on the outer greater coverts. Compared to the formative and juvenile plumage, definitive-plumage remiges had denser and bolder barring that seldom reached the rachis and were overall darker brown in color (Figure 3). Iris color was useful in aging Fulvous Wrens and was reddish-brown in birds with definitive plumage. Males and females were indistinguishable by plumage, and we were unable to use breeding criteria to distinguish between sexes.

Rust-and-yellow Tanager (*Thlypopsis ruficeps*). The preformative molt appeared to include only the lesser, median, and greater coverts, the alula covert, lesser alula, and carpal covert, but not the primary coverts, primary alula, rectrices, or remiges. Juvenile plumage was primarily dull yellow-olive above and below with a buffy-brown crown that was less extensive than definitive basic plumage; often limited to only the forehead.

Of three Rust-and-yellow Tanagers captured in formative plumage, two birds replaced two inner greater coverts while the other replaced five. Replaced greater coverts contrasted in size and appearance with retained outer greater coverts that were tapered, washed brown with faint yellow edging, and frequently quite worn during the time of

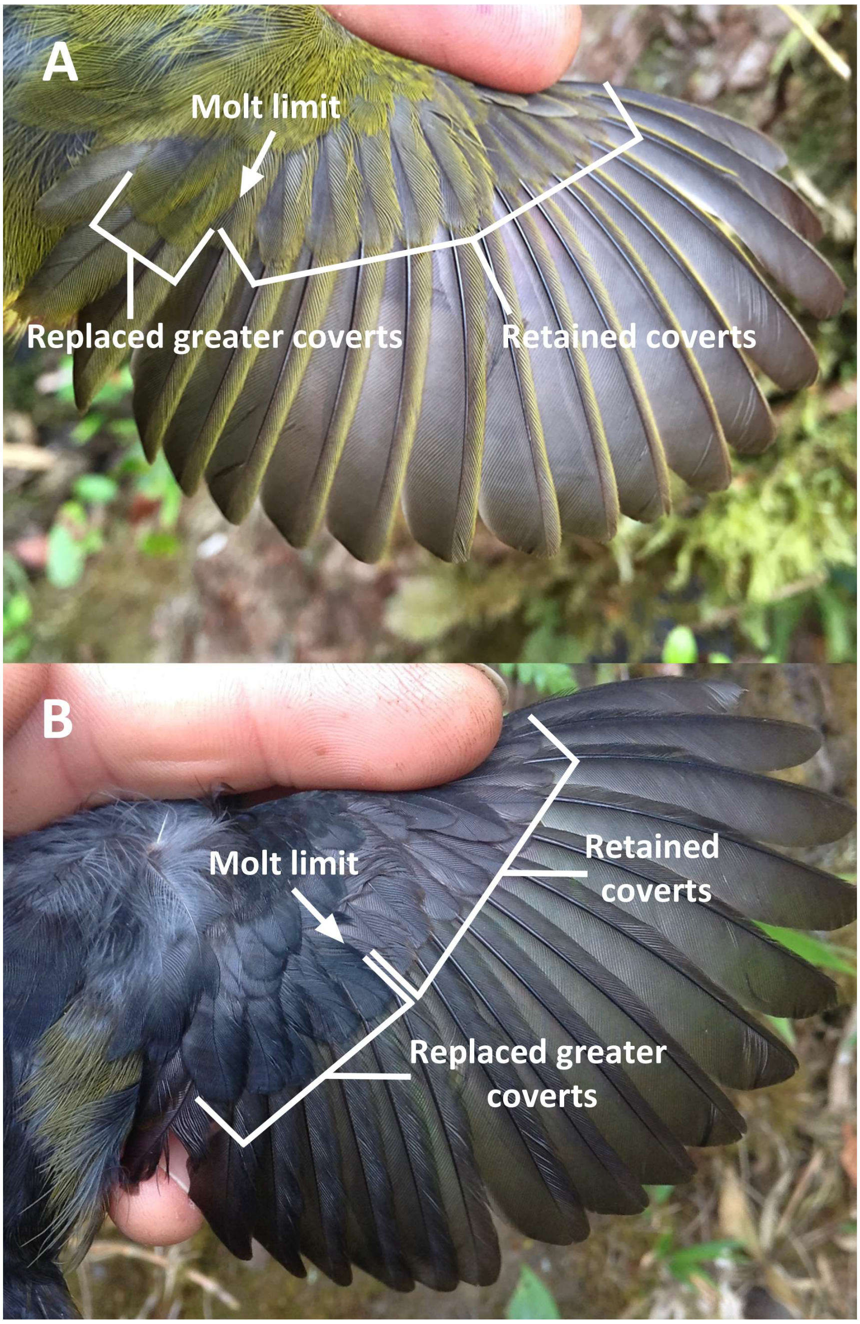

Figure 1. Molt limits within the greater coverts were the most commonly used feature to distinguish between formative and definitive basic plumages as seen in Rust-and-yellow Tanager (*Thlypopsis ruficeps*) (A) and Black-faced Brushfinch (*Atlapetes melanolaemus*) (B). Photo A: Jeremiah Kennedy, 25 September 2016, Wayqecha; photo B: Micah Scholer, 12 September 2015, Wayqecha.

year when our sampling occurred. Compared to the definitive basic plumage, the russet hood was less extensive and appeared duller, mottled with yellow, and seldom reached the back of the head or auriculars. Remiges and rectrices were typically heavily worn and more pointed relative to definitive basic plumage.

The definitive basic plumage had uniform primary and greater coverts with broad olive-green edging. The crown was also uniform orange in color and reached the back of the nape, auriculars, and cheeks. Definitive basic-plumage rectrices were broader and more truncate than the retained juvenile rectrices of the formative plumage. Males and females were indistinguishable by plumage, and we were unable to use breeding criteria to distinguish between sexes.

Blue-capped Tanager (*Thraupis cyanocephala*). The preformative molt included three to five inner greater coverts, one to three tertials, two to four rectrices, most to all median and lesser coverts, and the alula covert and lesser alula, but no primaries, primary coverts, or secondaries. Juvenile plum-

Table 1. Mean morphological measurements ± standard deviation for 10 avian species common to Andean forests of southeastern Peru. Length measurements are in millimeters; body mass is in grams; sample size is indicated in parentheses.

Species	Wing chord	Tail	Bill length	Bill width	Mass
Streak-necked Flycatcher (*Mionectes striaticollis*)	66.5 ± 4.3 (122)	51.4 ± 3.6 (119)	7.9 ± 0.5 (120)	4.0 ± 0.4 (120)	14.5 ± 1.8 (119)
Fulvous Wren (*Cinnycerthia fulva*)	57.3 ± 2.1 (75)	54.1 ± 3.2 (73)	9.6 ± 0.5 (72)	3.4 ± 0.2 (73)	17.4 ± 1.3 (75)
Rust-and-yellow Tanager (*Thlypopsis ruficeps*)	63.3 ± 4.3 (11)	52.2 ± 3.2 (11)	6.9 ± 0.3 (11)	3.1 ± 0.2 (11)	11.8 ± 0.7 (9)
Blue-capped Tanager (*Thraupis cyanocephala*)	83.1 ± 3.8 (18)	76.0 ± 3.6 (18)	8.9 ± 0.5 (16)	5.6 ± 0.6 (16)	37.4 ± 5.2 (18)
Scarlet-bellied Mountain-Tanager (*Anisognathus igniventris*)	85.5 ± 5.2 (50)	72.3 ± 3.5 (50)	7.8 ± 0.5 (32)	5.2 ± 0.5 (32)	34.4 ± 2.6 (47)
Black-throated Flowerpiercer (*Diglossa brunneiventris*)	65.3 ± 2.3 (13)	54.4 ± 2.5 (12)	7.9 ± 0.4 (13)	2.4 ± 0.1 (13)	14.5 ± 1.8 (119)
Masked Flowerpiercer (*Diglossa cyanea*)	74.0 ± 3.8 (98)	62.3 ± 3.4 (99)	11.4 ± 0.6 (97)	3.2 ± 0.3 (98)	14.8 ± 1.6 (82)
Black-faced Brushfinch (*Atlapetes melanolaemus*)	69.4 ± 3.5 (172)	71.3 ± 4.1 (160)	8.7 ± 0.5 (174)	4.9 ± 0.4 (174)	26.4 ± 3.2 (159)
Citrine Warbler (*Myiothlypis luteoviridis*)	64.3 ± 3.7 (87)	58.9 ± 3.2 (82)	8.2 ± 7.6 (83)	3.9 ± 0.4 (83)	14.8 ± 1.6 (82)
Pale-legged Warbler (*Myiothlypis signata*)	59.2 ± 2.5 (31)	56.7 ± 2.4 (31)	7.0 ± 0.5 (31)	4.0 ± 0.3 (31)	13.2 ± 0.9 (29)

Table 2. Select mean morphological measurements and their associated standard errors useful for classifying sex for five species of Neotropical passerines common to Andean forests of southeastern Peru. Length measurements are in millimeters; body mass is in grams; sample size is indicated in parentheses; *p*-values are Bonferroni-corrected.

Species	Measurement	Females		Males			
		Mean ± SD (N)	Range	Mean ± SD (N)	Range	df	*p*-value
Streak-necked Flycatcher (*Mionectes striaticollis*)	Wing chord	64.3 ± 3.0 (32)	59–72	70.6 ± 2.7 (34)	62–75	64	< 0.0001
	Tail	49.1 ± 2.8 (31)	43–55	54.5 ± 2.6 (34)	49–59	63	< 0.0001
	Mass	13.5 ± 1.2 (30)	11.8–16.6	16.1 ± 1.3 (34)	12.9–19.4	62	0.0060
Masked Flowerpiercer (*Diglossa cyanea*)	Wing chord	72.0 ± 3.5 (15)	66–77	77.3 ± 2.4 (26)	72–81	39	< 0.0001
	Tail	59.3 ± 2.9 (15)	55–65	63.8 ± 1.8 (26)	59–67	39	< 0.0001
	Mass	17.9 ± 1.9 (15)	14.3–20.8	19.0 ± 0.9 (26)	17.4–21.0	39	0.7560
Black-faced Brush-finch (*Atlapetes melanolaemus*)	Wing chord	68.2 ± 1.6 (29)	65–72	72.4 ± 2.6 (53)	66–82	80	< 0.0001
	Tail	69.7 ± 2.1 (28)	65–74	74.2 ± 3.1 (52)	67–80	78	< 0.0001
	Mass	26.8 ± 2.1 (24)	22.3–30.5	26.7 ± 1.5 (48)	23.7–31.9	70	0.9999
Citrine Warbler (*Myiothlypis luteoviridis*)	Wing chord	62.9 ± 2.8 (14)	56–66	67.1 ± 3.2 (8)	60–70	20	< 0.0001
	Tail	57.1 ± 3.2 (13)	50–60	60.7 ± 3.1 (8)	56–64	19	< 0.0001
	Mass	14.5 ± 1.0 (13)	12.7–15.9	17.1 ± 1.5 (7)	15.2–19.6	18	0.0110
Pale-legged Warbler (*Myiothlypis signata*)	Wing chord	56.5 ± 1.4 (6)	55–59	61.2 ± 1.1 (12)	59–63	16	< 0.0001
	Tail	54.5 ± 1.9 (6)	52–57	58.0 ± 2.1 (12)	55–61	16	0.1070
	Mass	12.9 ± 1.4 (6)	10.8–14.9	13.6 ± 1.0 (12)	12.7–15.3	16	0.9999

age median, greater, and primary coverts were thinly-edged with pale lemon-yellow and washed brown. The upper mandible of juvenile-plumage birds was gray and the black mask and blue head were duller with a grayish wash.

The formative plumage had a strong contrast between retained outer greater coverts and replaced inner greater coverts, which were dusky with a greenish wash and bright yellow-green edging. Rectrices often appeared tapered and relatively worn. The grayish upper mandible of juvenile-plumage individuals was sometimes still present during formative plumage with a variable amount of black extending from the base to the tip of the bill.

Figure 2. Definitive plumage of male and female Streak-necked Flycatchers (*Mionectes striaticollis*). Males in definitive basic plumage have a deeply notched ninth primary (A). Some females displayed a suspended molt retaining a variable number of scondaries (B). This female was originally banded in 2012 and was recaptured and photographed with the current molt pattern in 2014. Photo A: Barbara Reguera Alonso, 14 October 2014, Wayqecha; photo B: Barbara Reguera Alonso, 5 November 2014, Wayqecha.

Definitive-plumage individuals showed uniformly dusky greater and primary coverts with bright yellow-green edging and a greenish wash. The upper mandible was jet black. Males and females were indistinguishable by plumage, and we were unable to use breeding criteria to distinguish between sexes.

Scarlet-bellied Mountain-Tanager (*Anisognathus igniventris*). The preformative molt included zero to nine (generally one to six) inner greater coverts, the alula covert and lesser alula, most to all lesser and median coverts, zero to three tertials, a variable number of rectrices and, sometimes, the carpal covert. No primaries, primary coverts, or secondaries were found to have been replaced. The replacement of the alula covert and lesser alula was uncommon, but always coincided with replacement of tertials. Replaced feathers from the preformative and definitive prebasic molts were glossy-black with relatively broad iridescent navy-blue edging. Juvenile-plumage feathers were somewhat variable in color, ranging from washed brown to black with relatively little to no blue or turquoise-blue iridescent edging.

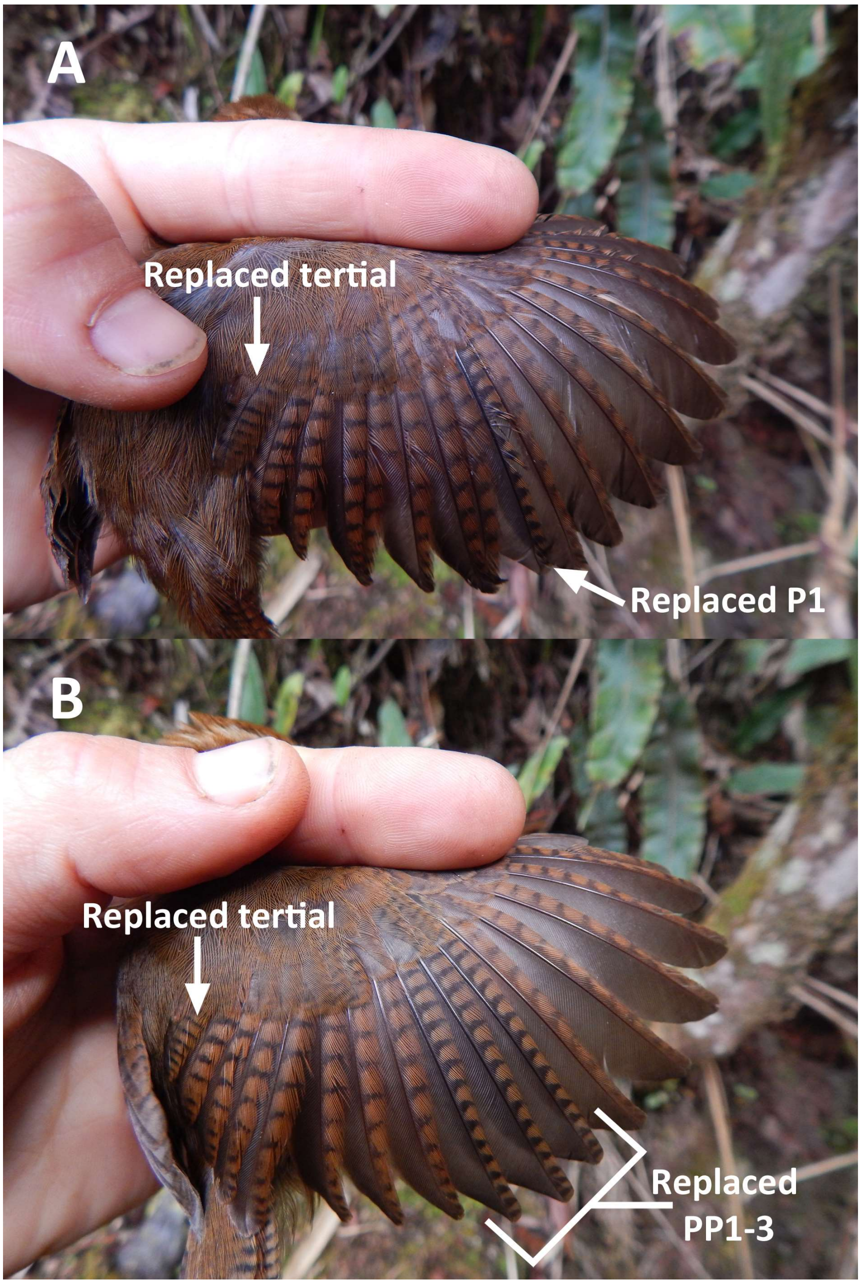

Figure 3. Formative plumage of two Fulvous Wrens (*Cinnycerthia fulva*). Incomplete preformative molts are common in this species resulting in the replacement of some remiges including one (A) to three (B) inner primaries as well as a variable number of tertial feathers. Photos: Barbara Reguera Alonso, 23 October 2014, Wayqecha.

The formative plumage was identified by contrast between darker and glossier black replaced inner greater coverts, which had broad iridescent navy-blue edging, and paler (often worn and washed gray) outer greater coverts with relatively narrow blue to turquoise-blue edging. A variable grayish wash to the black body plumage was also typical along with a paler blue shoulder patch and paler red belly and ear patch.

The definitive basic plumage had uniformly glossy-black greater and primary coverts with broad iridescent-blue edging. Overall, these individuals had a darker iridescent blue, brighter red and darker glossy-black body plumage than juvenile and formative-plumage individuals. Males and females were indistinguishable by plumage, and we were unable to use breeding criteria to distinguish between sexes.

Masked Flowerpiercer (*Diglossa cyanea*). The preformative molt included zero to nine greater coverts, zero to three tertials, some to all median and lesser coverts, zero to two alulas, but no rectrices, primary coverts, primaries or secondaries. The replacement of the alula covert and lesser alula was uncommon, but always coincided with the replacement of two to three tertials. Replaced feathers were dusky-black with extensive bright iridescent and deep-blue edging. Retained juvenile feathers ranged from dusky with relatively limited iridescent turquoise-blue edging to dusky-brown with limited matte-blue edging.

The formative plumage was easily identified by molt limits within the greater coverts (sometimes within the median coverts or between the greater and primary coverts) with the retained outer coverts contrasting markedly in wear and color with the darker, more extensively edged and fresher inner coverts. Formative-plumage birds also had a dusky-black mask, often with a grayish wash, and brownish-red to bright red iris.

The definitive basic plumage showed uniformly dark and fresh greater, median and primary coverts with extensive iridescent-blue edging. The mask was dark black, and the iris was scarlet red. Plumage characteristics should be used in concert with molt criteria as many formative-plumage individuals had relatively bright red irises with a jet-black mask. Males and females were indistinguishable by plumage, but were separable by statistically different morphological measurements; males averaged 7% longer wings and tails than females (Table 2).

Black-throated Flowerpiercer (*Diglossa brunneiventris*). The preformative molt included one (three of nine individuals) to six (one individual) greater coverts, usually two to three tertials (three individuals), and most to all median coverts. Primary coverts, rectrices, alulas, secondaries, and primaries were retained. The retained juvenile feathers were brown, narrow, tapered and often abraded with the addition of rusty to buffy-white tipping. Replaced feathers were broad, fresh, and dark dusky-black with gray tipping on greater coverts and tertials.

The formative plumage showed strong contrasts between the brown and pale-edged retained outer greater coverts and the black and gray-tipped replaced inner greater coverts. Retained body feathers were worn and brown resulting in a slightly mottled plumage. The head and back were mottled black and the breast and belly rusty-brown. Rectrices were brown and tapered with little to no rust edging.

The definitive basic plumage was characterized by uniformly black and gray-tipped greater coverts and broad black primary coverts. The crown and back were uniformly glossy-black and the chest was bright rusty-red. Rectrices were broad and black with little to no gray edging on the outer web. Males and females were indistinguishable by plumage, and we were unable to use breeding criteria to distinguish between sexes.

Black-faced Brushfinch (*Atlapetes melanolaemus*). The preformative molt included most or all lesser and median coverts, between one and nine greater coverts, and zero to three tertials. Occasionally, the carpal covert and alulas were also replaced along with the tertials. Rectrices were likely retained, although tail feathers of all age classes typically appeared ragged and were sometimes difficult to assign to a molt. The juvenile plumage was characterized by buff-tipping across the lesser, median, and greater coverts, a brown-wash on the chest and belly, a prominent fleshy yellow gape, and a chocolate-brown eye. The black feathers on the upperparts and remiges appeared drabber overall.

The preformative molt did not include primary and outer greater coverts, which were lighter, often buffy-tipped and lacked the luster of replaced definitive basic-plumage coverts. Retained rectrices were washed brown, narrower, and often much more worn, making it difficult to distinguish tail shape and color between age-classes (molt limits among the greater coverts was the most reliable aging criteria). As in juveniles, some formative-plumage individuals had a pale brown iris, which appeared to become redder with age. Most formative-plumage individuals had intermediate colored eyes somewhere between the pale brown iris of juveniles and the bright reddish-brown of definitive-plumage individuals.

The definitive basic plumage showed a lack of contrast within the greater coverts and uniformly-black back feathers, coverts, and remiges. Eye color was bright reddish-brown and the crest was always uniform rufous. Sexes were similar in all plumage aspects, but statistically different morphological measurements existed with males having wings and tails that averaged 6% longer than those of females (Table 2).

Citrine Warbler (*Myiothlypis luteoviridis*) and Pale-legged Warbler (*M. signata*). These two *Myiothlypis* warblers showed similar molt patterns and aging criteria. The preformative molt included the inner one to five greater coverts, but no remiges, tertials, primary coverts, or rectrices. Some median and lesser coverts were occasionally retained. Replaced feathers were dusky with greenish-yellow edging and relatively broad and fresh. Juveniles appeared drabber overall and had greater coverts washed brown with limited yellow edging.

The formative plumage was identified by contrast between the worn and brownish-washed outer greater coverts and replaced inner greater coverts, which were dusky with a greenish-yellow edging. A relatively limited and less distinct black crown and brow was a characteristic of formative- and juvenile-plumage individuals. However, we caution the use of crown length in assigning a molt cycle as the extent of black appeared to vary with both sex and age.

The definitive basic plumage showed uniformly fresh and dusky-centered coverts, rectrices and remiges. Rectrices were truncate without the brownish wash found in formative and juvenile individuals. A relatively extensive and distinct black crown and brow was typical. Although sexes were difficult to separate by plumage for both species, a combination of morphometric measurements were used to distinguish between male and female Citrine and Pale-legged Warblers. For both warbler species, wing chord was significantly longer in males compared to females (6% greater). For Citrine Warblers, differences in tail length and body mass were also statistically significant between sexes, with males averaging 6% and 15% larger than females, respectively (Table 2).

Care should be taken when identifying and aging these two species. Citrine Warblers showed darker legs, more extensive black on crown, a more distinct superciliary and tended to be larger overall. However, the crown color and pattern of formative Citrine Warblers and definitive basic Pale-legged Warblers were difficult to discern, and both species had relatively pale legs (pale orange in Citrine and pale pink in Pale-legged). Because of these similarities, plumage coloration should only be used in concert with molt criteria and morphometrics for aging and identification of these *Myiothlypis* warblers.

DISCUSSION

Our descriptions of molt and plumage for 10 species of Neotropical birds belonging to five families adds to the growing number of studies showing that tropical birds can be categorized by age and sex in a manner similar to that of their temperate counterparts (Wolfe et al. 2010, Johnson et al. 2011). We accomplished this mostly through the identification of molt limits acquired during each species' preformative molt and supported by characteristics such as feather wear, plumage aspect, and color of the eye and bill. All species under study showed a partial preformative molt apart from the Fulvous Wren, in which 27% of formative-plumage individuals captured underwent an incomplete preformative molt. Each species also exhibited a complete definitive prebasic molt with the possible exception of one species, Streak-necked Flycatcher*,* which may arrest or suspend molt in a portion of the population.

Although we did not detect any evidence of prealternate or auxiliary preformative molts, it is possible that such patterns exist, as has recently been suggested for related tropical taxa described in Mexico (Guallar et al. 2016). We caution that the extent of our sampling was not long enough to determine the complete molt phenology for the above described species. Our results should therefore be interpreted as preliminary with the goal of expanding sampling to include the non-breeding season. Unfortunately, such sampling is often hampered by heavy rains characteristic of many tropical locations during this time period, as was the case for our study.

For the Streak-necked Flycatcher, we found evidence of an arrested or suspended definitive prebasic molt. In arrested molts, feather replacement is interrupted before completion and molt resumes at its point of initiation (i.e., molt center) in the subsequent molt. In comparison, suspended molts are temporary cessations that continue replacement of not yet replaced feathers, starting from the point at which the last molt terminated, rather than beginning from the original molt center. We find the possibility of an arrested or suspended molt likely for several reasons. First, relatively few cases (< 10% of captured individuals) were documented and occurred only in females in definitive basic plumage despite there being a similar number of males identified in our sample (31 females and 34 males; Table 2). Male Streak-necked Flycatchers often form exploded leks (Greeney et al. 2006). As such, the majority of nest attendance is presumed to be carried out by females. Under certain conditions, the energetically demanding tasks of incubation and rearing young may cause females to stop active molt in order to invest energy into breeding (Pyle 2005, 2013). This may explain the occurrence of these observed molt patterns in the definitive molt cycle of females and not males. Second, one female originally captured in 2012, had retained the 10th primary and the third, fifth, and sixth secondaries when it was recaptured in 2014 (Figure 2B). This same individual was recaptured again in 2015 with uniform primaries and secondaries, indicating it had sub-sequently undergone a complete definitive prebasic molt. Because this molt pattern was observed in a small portion of individuals, only occurred in females, and appeared in individuals that also underwent complete definitive prebasic molts, we suggest that it likely represents an arrested or suspended molt to accommodate breeding. Although similar patterns have been documented in other tropical bird taxa with protracted breeding seasons (Freed & Cann 2012, Pyle 2013, Pyle et al. 2016), our short duration of sampling does not rule out the possibility that this is an incomplete definitive prebasic molt exhibited by a specific age and sex.

Morphological measurements were useful in distinguishing between sexes for a portion of the population of Streak-necked Flycatcher (53% of individuals of known sex were successfully classified as males or females), Masked Flowerpiercer (59%), Black-faced Brushfinch (41%), Citrine Warbler (68%), and Pale-legged Warbler (89%). With the exception of the Streak-necked Flycatcher, we were able to confirm the sex of individuals only by the presence of breeding characters (e.g., brood patches or cloacal protuberances). Thus, our ability to distinguish between males and females using morphometrics was largely limited by the number of actively breeding individuals. For example, no cloacal protuberances were documented for Fulvous Wren, Rust-and-yellow Tanager, or Blue-capped Tanager. It is possible that males of these species do not develop obvious secondary sexual characteristics to allow for sex classification or that our sampling occurred during an interval in which most males were not actively breeding. We also acknowledge the possibility that no males of any of these species were captured, although we find this unlikely for at least the Fulvous Wren, of which 75 individuals have been captured. Future sampling outside of the months we focused netting efforts would help clarify whether difference in such morphometric characteristics exist between sexes, particularly for species for which we were unable to confirm the presence of males.

We hope that this contribution to the growing body of knowledge on tropical bird molt and utilization of aging and sexing tools motivates similar studies in the future. Ultimately, an increased knowledge of molt patterns and age and sex classification will serve to better our understanding of demographics and population dynamics in Neotropical birds.

ACKNOWLEDGMENTS

We thank the many volunteers from the Manu Bird Project, who assisted with data collection. In particular, Barbara Reguera Alonso for her inspiration in the field and her many useful photos of molt stages. Wayne Arendt and Erik Johnson reviewed an earlier draft of this manuscript and greatly improved its focus and clarity. Grants from the North American Bird Banding Association and Werner and Hildegard Hesse Research Award in Ornithology and the University of British Columbia Zoology department provided funding for this study. We thank our host research station Wayqecha, especially Robinson Palomino, as well as the Asociación para la Conservación de la Cuenca Amazónica for providing us with accommodations, cooperation, and comradery. We are also grateful to the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) for permission to work in the Manu Park buffer zone.

REFERENCES

Cox, AW, FR Thompson, AS Cox & J Faaborg (2014) Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management* 78: 183–193.

Figuerola, J, R Jovani & D Sol (2001) Age-related habitat segregation by Robins *Erithacus rubecula* during winter. *Bird Study* 48: 252–255.

Freed, LA & RL Cann (2012) Changes in timing, duration and symmetry of molt of Hawaiian forest birds. *PLoS One* 7: e29834.

Girardin, CAJ, Y Malhi, KJ Feeley, J Rapp, MR Silman, P Meir, WH Huasco, N Salinas, M Mamani, JE Silva-Espejo, KG Cabera, WF Rios, DB Metcalfe, CE Doughty & LEOC Aragão (2014) Seasonality of above-ground net primary productivity along an Andean altitudinal transect in Peru. *Journal of Tropical Ecology* 30: 503–519.

Greeney, HF, C Dingle, RC Dobbs & PR Martin (2006) Natural history of Streak-necked Flycatcher *Mionectes striaticollis* in north-east Ecuador. *Cotinga* 25: 59–64.

Guallar, S, E Santana, S Contreras, H Verdugo, & A Gallés (2009) Paseriformes del occidente de México: morfometría, data-ción y sexado. *Monografies del Museu de Ciències Naturals* 5.

Guallar, SX, A Ruiz-Sánchez, R Rueda-Hernández & P Pyle (2016) Molt strategies of ten Neotropical forest passerine species. *Wilson Journal of Ornithology* 128: 543–555.

Hernández, A (2012) Molt patterns and sex and age criteria for selected landbirds of southwest Colombia. *Ornitología Neotropical* 23: 215–223.

Hosner, PA, MJ Andersen, MB Robbins, A Urbay-Tello, L Cueto-Aparicio, K Verde-Guerra, LA Sánchez-González, AG Navarro-Sigüenza, RL Boyd, J Núñez, J Tiravanti, M Combe, H L Owens & A Townsend Peterson (2015) Avifaunal surveys of the upper Apurímac River Valley, Ayacucho and Cuzco Departments, Peru: new distributional records and biogeographic, taxonomic, and conservation implications. *Wilson Journal of Ornithology* 127: 563–581.

Howell, SNG, C Corben, P Pyle & DI Rogers (2003) The first basic problem: a review of molt and plumage homologies. *The Condor* 105: 635–653.

Humphrey, PS & KC Parkes (1959) An approach to the study of molts and plumages. *The Auk* 76: 1–31.

Jankowski, JE, CL Merkord, WF Rios, KG Cabrera, NS Revilla, & MR Silman (2013) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography* 40: 950–962.

Jenni, L & R Winkler (1994) *Moult and ageing of European passerines*. Academic Press, New York, New York, USA.

Johnson EI, JD Wolfe, TB Ryder & P Pyle (2011) Modifications to a molt-based ageing system proposed by Wolfe et al. (2010). *Journal of Field Ornithology* 82: 422–424.

Johnson, EI & JD Wolfe (2014) Thamnophilidae (antbird) molt strategies in a central Amazonian rainforest. *Wilson Journal of Ornithology* 126: 451–462.

Johnson, EI & JD Wolfe (2017) *Molt in Neotropical birds. Life history and aging criteria*. CRC Press, Boca Raton, Florida, USA.

Morton, ES (1990) Habitat segregation by sex in the Hooded Warbler: experiments on proximate causation and discussion of its evolution. *American Naturalist* 135: 319–333.

Pagen, RW, FR Thompson III & DE Burhans (2000) Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. *The Condor* 102: 738–747.

Pyle, P (1997) *Identification guide to North American birds, part 1*. Slate Creek Press, Bolinas, California, USA.

Pyle, P (2005) Remigial molt patterns in North American Falconiformes as related to age, sex, breeding status, and life-history strategies. *The Condor* 107: 823–834.

Pyle, P (2013) Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconiformes) and parrots (Psittaciformes). *The Condor* 115: 593–602.

Pyle, P, A McAndrews, P Vélez, RL Wilkerson, RB Siegel & DF DeSante (2004) Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *Journal of Field Ornithology* 75: 136–145.

Pyle, P, K Tranquillo, K Kayano & N Arcilla (2016) Molt patterns, age criteria, and molt-breeding dynamics in American Samoan landbirds. *Wilson Journal of Ornithology* 128: 56–69.

Radley, P, AL Crary, J Bradley, C Carter & P Pyle (2011) Molt patterns, biometrics, and age and gender classification of landbirds on Saipan, Northern Mariana Islands. *Wilson Journal of Ornithology* 123: 588–594.

Sillett, TS & RT Holmes (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71: 296–308.

Tarwater, CE, RE Ricklefs, JD Maddox & JD Brawn (2011) Pre-reproductive survival in a tropical bird and its implications for avian life histories. *Ecology* 92: 1271–1281.

Terborgh, J, SK Robinson, TA Parker III, CA Munn & N Pierpont (1990) Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60: 213–238.

Tórrez, MA & WJ Arendt (2017) *La muda en especies de aves selectas de Nicaragua.* 1st ed. UCA Publicaciones, Managua, Nicaragua.

Vitz, AC & AD Rodewald (2006) Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127: 477–486.

Wolfe, JD, RB Chandler & DI King (2009a) Molt patterns, age and sex criteria for selected highland Costa Rican resident landbirds. *Ornitología Neotropical* 20: 1–9.

Wolfe, JD, P Pyle & CJ Ralph (2009b) Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. *Wilson Journal of Ornithology* 121: 556–567.

Wolfe, JD, TB Ryder & P Pyle (2010) Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81: 186–194.

Zar, JH (1996) *Biostatistical analysis*. 3rd ed. Prentice Hall, Upper Saddle River, New Jersey, USA.