ORNITOLOGÍA NEOTROPICAL
SPECIAL ISSUE (2018) 29: S51–S61

ORIGINAL ARTICLE

Sociedad de Ornitología Neotropical

AGE DETERMINATION BASED ON MOLT PATTERNS AND SKULL OSSIFICATION IN THE BLUE-AND-YELLOW TANAGER (*PIPRAEIDEA BONARIENSIS*)

Alexis Díaz[1,2,3] · Flor Hernández[1,4] · Luis Alza[1,3] · Kevin Chumpitaz[1] · Julio Salvador[1] · Erika Berrocal[1] · Yaquelin Tenorio[1,2] · Tania Poma[1] · Celeste Santos[1] · José Iannacone[2]

[1] Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita No 105, Dpto. 202, Urb. Huertos de San Antonio, Surco Lima, Perú.

[2] Laboratorio de Biodiversidad Animal, Facultad de Ciencias Naturales y Matemática, Universidad Nacional Federico Villarreal (UNFV), Av. Río Chepén s/n, El Agustino, Lima, Perú.

[3] Department of Biology, University of Miami, Coral Gables, FL 33146, USA.

[4] Department of Biological Sciences, University of Texas El Paso, El Paso, TX 79968, USA.

E-mail: Alexis Díaz · alexis.diaz@corbidi.org

Abstract · We studied molt patterns and age determination based on molt limits, plumage criteria, and skull ossification for the Blue-and-yellow Tanager (*Pipraeidea bonariensis*), a passerine that is commonly distributed along the western slope of the Peruvian Andes. Through careful examination of live individuals in the hand and museum specimens, we suggest that *P. bonariensis* exhibits a complex alternate strategy with partial preformative and prealternate molts during its first cycle, a complete definitive prebasic molt, and presumably a partial definitive prealternate molt starting with its second cycle. We established the age in 68% of captured individuals using the skulling technique. Most individuals of *P. bonariensis* were recorded with fully ossified skulls during their preformative molts, whereas some adults in basic plumage had retained small, unossified windows. Our results corroborate those reported for related Neotropical taxa and provide important guidelines that facilitate an accurate and rapid technique for aging and sexing Neotropical tanagers in the hand, an essential requirement in demographic studies and long-term banding projects.

Resumen · Determinación de la edad basado en patrones de muda y la osificación craneal de la Tangara azul y amarilla (*Pipraeidea bonariensis*)
Estudiamos los patrones de muda y la determinación de la edad basados en la identificación de límites de muda, apariencia del plumaje y la osificación del cráneo para la Tangara azul y amarilla (*Pipraeidea bonariensis*), una ave paserina que se distribuye comúnmente a lo largo de la vertiente occidental de los Andes peruanos. A través de un examen cuidadoso de individuos vivos en especímenes de mano y de museo, sugerimos que *P. bonariensis* exhibe una estrategia alterna compleja con una muda preformativa y prealterna parcial en su primer ciclo, una muda prebásica definitiva completa y presumiblemente una muda prealterna definitiva parcial a partir del segundo ciclo. Establecimos la edad en el 68% de los individuos capturados utilizando la técnica de observación del cráneo. Además, la mayoría de individuos de *P. bonariensis* lograron culminar dicho proceso de osificación durante la muda preformativa. Sin embargo, algunos individuos en plumaje básico definitivo pueden retener pequeñas ventanas no osificadas. Los resultados confirman lo reportado para otros taxa relacionados en las zonas tropicales y constituyen una importante herramienta que asegura una certera y rápida identificación de la edad y sexo para tangaras de los trópicos en mano, requisito indispensable en estudios demográficos y programas de anillamiento y monitoreo a largo plazo.

Key words: Complex alternate molt strategy · Molt extent · Peru · Prealternate molt · Preformative molt · Thraupidae

INTRODUCTION

Population monitoring and demographic studies provide valuable information to assess trends and changes in the abundance of birds in reference to space and time. However, criteria to estimate the age and sex of individuals within the population are needed to achieve a detailed understanding of avian demography (Hernández

Receipt 26 June 2016 · First decision 7 November 2016 · Acceptance 22 May 2018 · Online publication 30 May 2018

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

2012). Knowledge of molt strategies has been a useful prerequisite to developing accurate and consistent criteria to estimate the age and gender of most species inhabiting temperate regions (Svensson 1992, Pyle 1997a, 1997b). Unfortunately, the information available about molt strategies in Neotropical birds is still limited (Ryder & Wolfe 2009, Bridge 2011, Wolfe & Pyle 2012, Johnson & Wolfe 2018).

Most of the studies about molt in Neotropical resident bird species have been focused on the timing of molt in relation to other events of the annual cycle as phenology (Poulin et al. 1992) and reproduction (Foster 1975, Piratelli et al. 2000, Marini & Durães 2001, Mallet-Rodrigues 2005, Moreno-Palacios et al. 2013). More recently, other inherent attributes of molt have been studied, such as its duration, extent, and sequence of plumages (Pyle et al. 2004, Ryder & Durães 2005, Ryder & Wolfe 2009; Wolfe et al. 2009a, 2009b; Botero-Delgadillo et al. 2012, Gómez et al. 2012, Ruíz-Sánchez et al. 2012, Guallar et al. 2014, 2016, in press; Johnson & Wolfe 2018). Additionally, the study of molt in the tropics is advancing with the new molt cycle-based ('Wolfe-Ryder-Pyle') age classification system that overcomes the problems of using the calendar-based system, widely used in temperate zone birds but diffuse for tropical or subtropical regions where breeding and fledging can occur across calendar years (Wolfe et al. 2010, Pyle et al. 2015, Johnson & Wolfe 2018).

The extent of the skull ossification is another method for age determination (Pyle 1997b). In juvenile birds, the skull bone is a thin and transparent layer, but as the ossification progresses, a second layer grows below the first one, and between both layers columns of bone separated by air pockets form (Dwight 1900). The extent of skull ossification would offer a certain degree of age accuracy depending on the species and the time of the year (Weisshaupt & Vilches-Morales 2010). For most migrant and resident passerine species from temperate zones, the progress of skull ossification is considered a reliable criterion for recognizing young birds (Eaton 2001, Pyle et al. 2015); however, skull ossification patterns in Neotropical resident species are poorly understood (Pyle et al. 2015). In addition, skull ossification in some species can be difficult to assess, leading to errors or large proportions of uncertain cases.

Tanagers in the family Thraupidae are a diverse tropical group of passerines representing 12% of the Neotropical avifauna (Burns et al. 2014). The family displays a wide range of plumage colors and patterns, foraging behaviors, vocalizations, ecotypes, and habitat preferences (Burns 1997). Due to its wide diversity and distribution, the Neotropical tanagers present different molting strategies that include the Complex Basic Strategy (CBS) and Complex Alternate Strategy (CAS), with a variable extent for preformative molt and few records of partial prealternate molt (Ryder & Wolfe 2009). Moreover, some genera exhibit a partial performative molt; others exhibit a complete preformative molt, and for most genera, the existence of prealternate molt remains unknown. Therefore, the objective of this study was to document the molt patterns, plumage sequences and the relationship between molt cycle-based age categories, and skull ossification of the Blue-and-yellow Tanager (*Pipraeidea bonariensis*). This tanager species is sexually dichromatic and is widely distributed in South America. In Peru, it is found in dry montane scrub habitats between 2000 and 4200 m a.s.l. along the Andes (Schulenberg et al. 2010). Results presented here are based on specimens obtained from museum collections and banding data from a study of bird ecology in the highlands around Lima, Peru.

METHODS

The study was carried out at the Estación Biológica Río Santa Eulalia – Centro de Ornitología y Biodiversidad (11.74406°S, 76.60875°W, 2300 m a.s.l.), located at the district of San Pedro de Casta, Province of Huarochirí, department of Lima in the western Andes of Peru. The predominant habitat type is tropical montane desert scrub intermixed with a mosaic of agroscapes (MINAM 2012). From June 2012 to May 2015, 10 standard mist nets (12 m in length with 36 mm mesh) were used to capture birds. The nets were opened between 06:00 h and 18:00 h (EST) during two days per month, ensuring a monthly effort of 120 net-hours (Moreno-Palacios et al. 2014). All birds were marked with a uniquely numbered aluminum leg band, processed and released following international standards (NABC 2001). Sex was assessed by plumage coloration and the presence of breeding characters (brood patch and cloacal protuberance) following Pyle (1997b). Males can be identified by their blue head, wings, and tail black with blue edging, olive back, and yellow underparts and rump; females, for its part, are similar but with yellow-ochre underparts and less colorful overall (Schulenberg et al. 2010). Age was assessed, when possible, through identification of molt limits, plumage criteria, and extent of skull ossification (Mulvihill & Winstead 1997; Pyle 1997a, 1997b; Froehlich 2003). Age was categorized according to the molt cycle-based aging system proposed by Wolfe et al. (2010), refined by Johnson et al. (2011) and based on the molt terminology of Humphrey & Parkes (1959) as modified by Howell et al. (2003). Banding data collected included body molt, wing molt, molt limits, skull ossification and photographs of open wings to analyze and document molt patterns.

Feather-tract and wing-molt pattern terminology follow those of Pyle (1997b) and Guallar et al. (2018), respectively. Rectrices (rects), primaries (pp), secondaries (ss), and their coverts are considered as "inner" and "outer" depending on their position in relation to the body of the bird. For wing-molt patterns, "complete" indicates the entire replacement of feathers; "eccentric" refers to an almost complete replacement with retention of inner primaries, outer secondaries and primary coverts; "general" refers to a partial

Table 1. Sample sizes used to study molt in the Blue-and-yellow Tanager (*Pipraeidea bonariensis*) from Peru. [1]FPJ= First cycle, first prebasic (prejuvenile) molt. FCJ = First cycle, first basic (juvenile) plumage. FPF = First cycle, preformative molt. FCF = First cycle, formative plumage. FPA = First cycle, first prealternate molt. FCA = First cycle, first alternate plumage. FCU = First cycle, unknown plumage. SPB = Second cycle, second prebasic molt. DPB = Definitive cycle, definitive prebasic molt. DCB = Definitive cycle, definitive basic plumage. DPA = Definitive cycle, prealternate molt. DCA = Definitive cycle, alternate plumage. DCU = Definitive cycle, unknown plumage. UPU = Unknown molt cycle, undergoing molt. UCU = Unknown cycle, unknown plumage. UUU = Unknown molt cycle, unknown molt status.

Cycle code[1]	FPJ	FCJ	FPF	FCF	FPA	FCA	FCU	SPB	DPB	DCB	DPA	DCA	DCU	UPU	UCU	UUU
Field captures	2	6	25	30	0	1	5	4	22	36	0	0	7	9	28	5
Museum specimens	0	0	0	3	0	0	0	1	0	8	0	0	0	0	0	0

Table 2. Number of individuals that replaced particular feathers tracts during the preformative molt of the Blue-and-yellow Tanager (*Pipraeidea bonariensis)* from Peru. Abbreviations (following Pyle 1997b): gr covs = greater coverts; terts = tertials; rects = rectrices.

Replaced feather tracts	0 gr covs	1–8 gr covs	9 gr covs	0 terts	1–2 terts	3 terts	0 rects	1–5 pairs of rects	6 pairs of rects
Captured birds	0	25	5	9	12	2	5	4	3
Museum specimens	0	2	1	1	2	0	0	2	1

replacement that prioritizes feathers from leading edge (secondary coverts, alula, less frequently tertials) over those of trailing edge of the wing (secondaries, primaries or primary coverts) and with the tertials replaced only if all coverts are molted; "proximal" is similar to the general pattern but tertials are replaced with retention of outer secondary coverts; "inverted" refers to a partial replacement that prioritizes feathers from trailing edge (tertials, secondaries, and greater coverts) over those leading edge of the wing (median and lesser coverts); "limited" refers to a partial replacement that only affects the lesser and median coverts, and ''reduced' indicates only replacement of a few tertials or greater coverts near the body. Color descriptions follow recommendations by Pyle (1997b). We complemented information obtained from fieldwork with data gathered on museum specimens from the John O'Neill Ornithological Collection of CORBIDI.

For skull ossification, we examined 117 individuals captured in mist nets. Each skull was examined by parting the head feathers and, if necessary, by wetting them slightly, as described by Svensson (1992) and Pyle (1997b). We quantified the amount of skull pneumatization using the ossification key from Ralph et al. (2012), in which a rating of zero to six is assigned for every individual. The score zero is for birds with non-ossified skull and six for birds with complete ossified skulls. The possible association between degree of skull ossification and age categories was evaluated using Chi-square test.

RESULTS

In total, 180 individuals of *P. bonariensis* were captured during 5400 net-hours (3.3 ind./100 h). Captures included 58 males, 56 females, and 66 individuals of undetermined sex. Thirteen molt-cycle-based age categories were recorded for captured birds. Of this total, five categories corresponded to individuals from which cycle, molt, or plumage status could not be accurately determined during examination (FCU, DCU, UCU, UPU, and UUU). In addition, 12 museum specimens were examined, corresponding to nine males and three females, distributed among three age categories (Table 1).

Juveniles undergoing their first prebasic (prejuvenile) molt (FPJ) were recorded at our study site in June. Birds in this age class are recognized by the simultaneous growth of body and flight feathers, a well-known pattern found in passerines. A dull bluish-gray head, pale yellow underparts, olive-green back, and a dark yellowish-brown rump characterize juveniles in first basic (juvenile) plumage (FCJ), which was found at our study site from May to July. Pale yellow coloration is also present in other body feathers such as the edge of secondary coverts (inner lesser coverts and all median and greater coverts). In addition, the alula, outer lesser coverts, and flight feathers exhibit a bluish edge, which is more evident in the secondaries (Figure 1). Many of the above features can be easily observed among young tanagers in juvenile plumage. Over time, the bluish edging is lost through

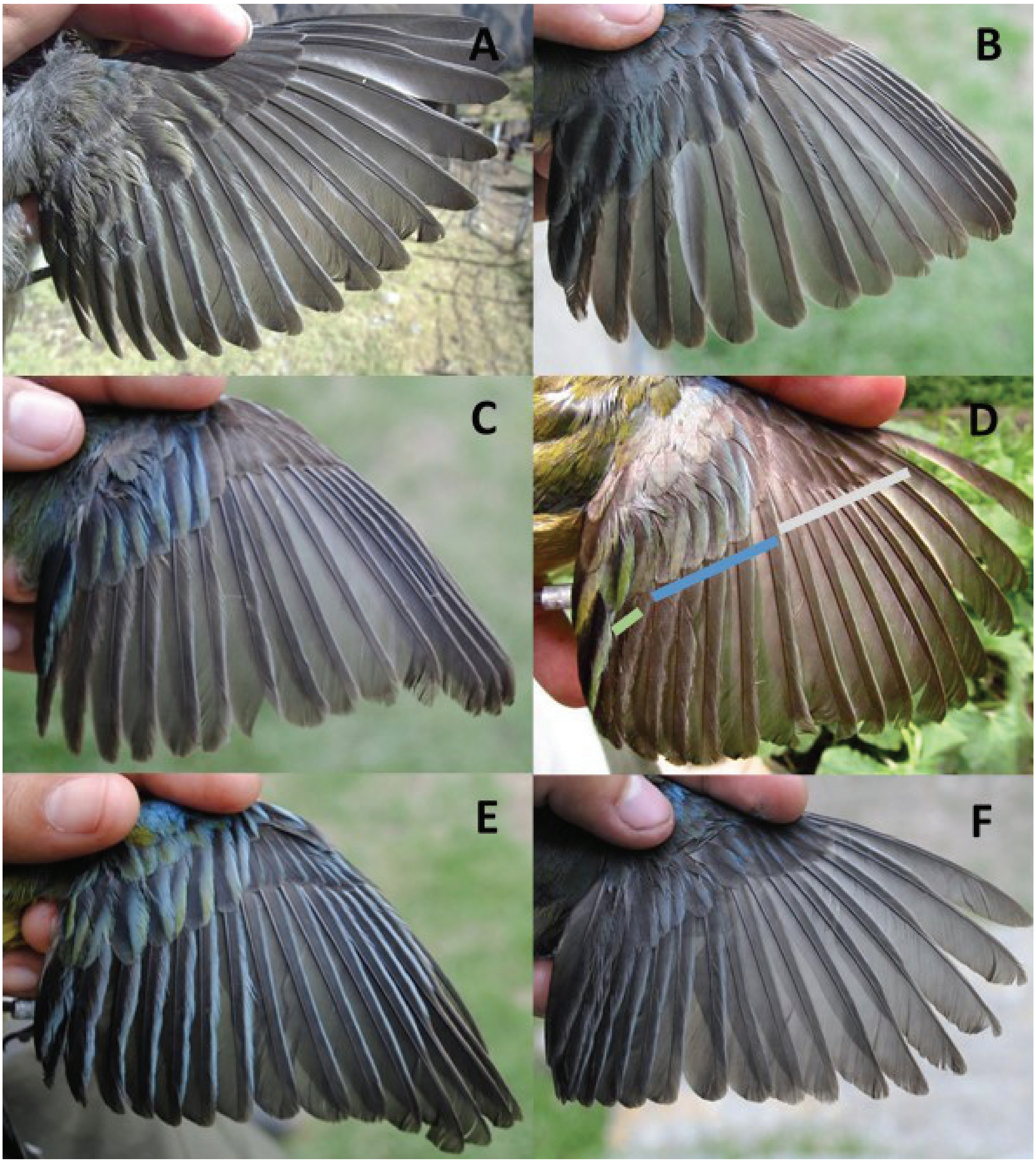

Figure 1. Representative images of different plumages of the Blue-and-yellow Tanager (*Pipraeidea bonariensis*) captured in Peru. Each colored line insert represents one feather generation and codes represent band numbers. A) First basic (juvenile) plumage, C002628, 25 June 2012 (photo: F. Hernández). B) Formative plumage (Female), D002466, 21 December 2013 (photo: Y. Tenorio). C) Formative plumage (Male), C002847, 28 July 2013 (photo: E. Berrocal). D) Possible first alternate plumage (Male), D001665, 14 March 2015 (photo: J. Salvador). E) Definitive basic plumage (Male), C002467, 21 December 2013 (photo: K. Chumpitaz). F) Definitive basic plumage (Female), C002627, 12 April 2014 (photo: T. Poma).

feather wear and plumage discoloration becomes evident. Sex differences were not evident in this age category.

The preformative molt (FPF) followed a partial replacement with the proximal pattern being more prevalent than the general pattern among all individuals captured. Birds undergoing this molt have been recorded from June to January at our study site. The FPF included most body feathers, all median and lesser coverts, and at least one (83% of individuals) to all (17% of individuals) greater coverts. In addition, no (39% of individuals) to all (7% of individuals) of the tertials, and no (42% of individuals) to all (25% of individuals) of the rectrices were replaced as a result of the FPF molt according to available information from captured birds (Table 2). Formative-plumaged birds

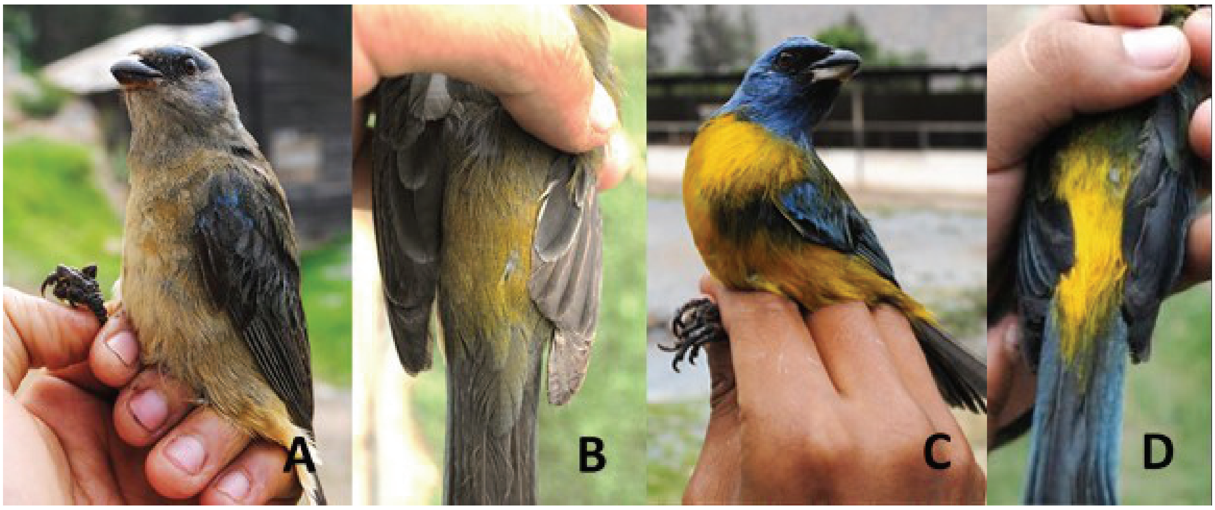

Figure 2. Comparison of definitive basic plumage between sexes of the Blue-and-yellow Tanager (*Pipraeidea bonariensis*) captured in Peru. Codes represent band numbers. Definitive Cycle Basic female, C002466, 21 December 2013 (photo: A. Díaz): A) Body plumage, B) Rump. Definitive Cycle Basic male, C002847, 25 October 2014 (photo: A. Díaz): C) Body plumage, D) Rump.

(FCF), recorded from July to March at our study site, were identified by the presence of molt limits, which occur among the greater coverts or between greater coverts, and primary coverts. Replaced greater coverts in females resemble those of males, but in the males, the greater coverts have a blue and pale yellow coloration at the leading edge of each feather. The FCF can also be characterized by retained rectrices, which are often tapered and worn.

Only one male was recorded in March in its first alternate plumage (FCA) as consequence of a partial replacement following the inverted wing-molt pattern. The bird was recognized by the presence of three generations of feathers and two molt limits as a consequence of the preformative and first prealternate molt, respectively (see Pyle 1997a, 1997b). Some body feathers from the head, breast, scapulars and the innermost greater covert were replaced by brighter ones during first prealternate molt. This first-alternate greater covert also contrasted with the retained (formative) greater coverts, being less worn and with a greenish edge. The inner two tertials were also replaced during this first prealternate molt (Figure 1).

The adult prebasic molt (DPB), recorded from May to September at our study site, was complete and proceeded in typical sequence. Individuals undergoing their second prebasic molt (SPB) were recognized by their retained and worn juvenile flight feathers, which distinctly contrasted with those that had been replaced (second basic); the latter appeared less worn, brighter, and truncated. Definitive basic plumage (DCB), recorded from July to May, is obtained after the SPB. DCB females have pale yellow underparts and a dark yellow rump, whereas DCB males have bright yellow underparts and rump (Figure 2). In addition, all flight feathers (especially primary coverts) and secondary coverts are well-defined black feathers in males and slightly less bright colored in females; both with a distal blue leading edge, which is not apparent on juvenile primary coverts retained through the first molt cycle. Relatively fresh and truncated rectrices also characterize DCB individuals.

Skull ossification followed the typical median line pattern (Pyle 1997b) and was useful for determining age in 68% of individuals examined (n = 117). Skull ossification showed a significant association with the different age categories considered in our analysis ($c^2 = 124.283$, df = 30, $P < 0.05$). All FCJ birds showed low ossification scores (Oss = 2, < 1/3 ossified), whereas 25% of FPF individuals shown fully ossified skulls (Figure 3). Banding data related to these cases of early skull completion (light body molt, moderate feather wear, and capture dates between November and January) may suggest that this could have happened late in the FPF. Moreover, 78.1% of DCB individuals had completely ossified skulls whereas the remaining 21.9% retained only small "windows" in the skull (4 ≤ Oss ≤ 5, > 70% of the skull ossified) (Figure 3).

DISCUSSION

Our observations suggest that *P. bonariensis*, in the western slope of the central Andes, may exhibit a complex-alternate molt strategy with a preformative and a prealternate molt inserted during its first cycle, and complete definitive prebasic molt, and presumably a partial definitive prealternate molt starting in its second cycle. This strategy has also been documented in 28.2% of the North American passerines studied so far, especially in Neartic-Neotropic migrants (Wolfe & Pyle 2012), and less commonly for Neotropical resident species (Ryder & Wolfe 2009, Wolfe & Pyle 2012, Johnson & Wolfe 2018). Moreover, the occurrence of this molt strategy is often associated with migrate behavior and prolonged solar exposure (Pyle & Kayhart 2010).

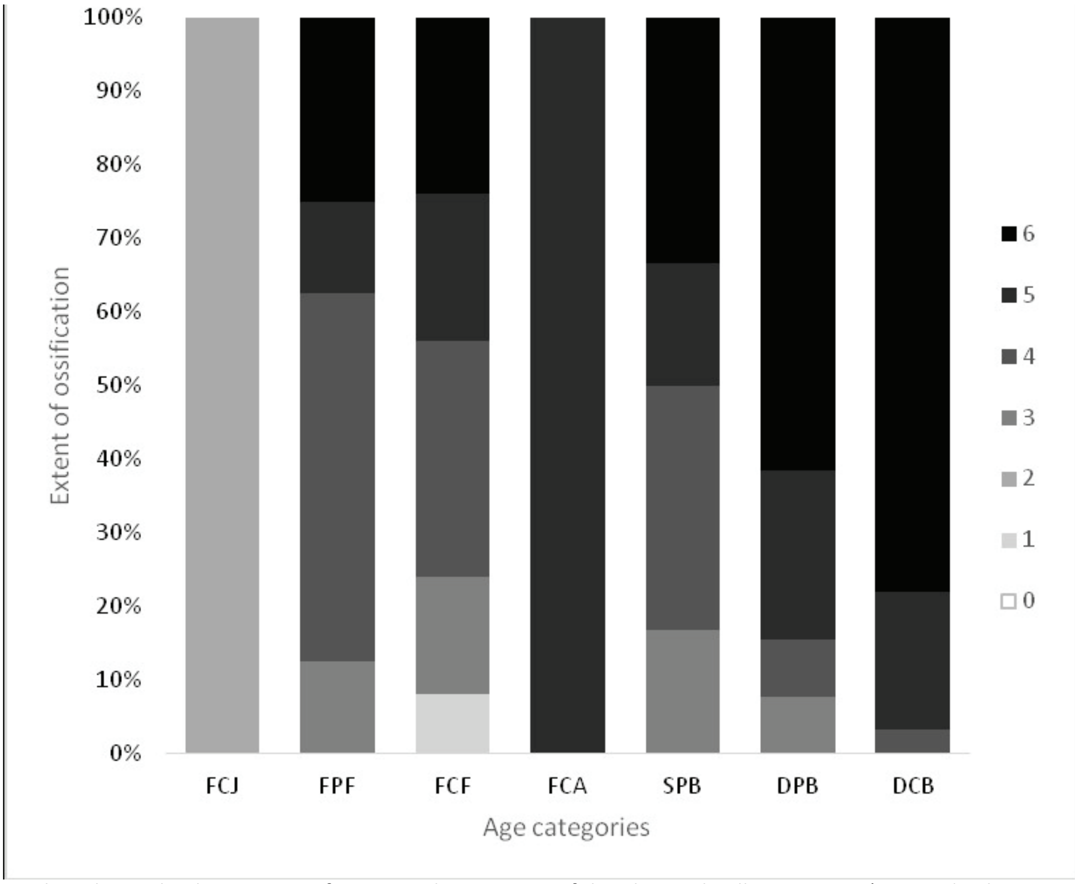

Figure 3. The relationship between ossification and age groups of the Blue-and-yellow Tanager (*Pipraeidea bonariensis*) captured in Peru. See text and Table 1 for definitions of molt cycle-based age codes. Gray scales represent extent of skull ossification.

The partial preformative molt of *P. bonariensis*, documented in this study is consistent with the extent of this molt for most tanagers and other Thraupidae species in the Neotropic (Ryder & Wolfe 2009) (Figure 4). Tropical birds molt most of their body feathers, including lesser and median coverts and a variable number of greater coverts, whereas flight feathers are retained (Ryder & Wolfe 2009, Botero-Delgadillo et al. 2012, Gómez et al. 2012, Hernández 2012, Pyle et al. 2015) (Table 3). This may reflect the influence of phylogenetic history on molt and its evolution among temperate and tropical taxa (Wolfe & Pyle 2012). In some other cases, molt patterns are also influenced by other factors such as environmental constraints (climate) and physiological events (timing of the breeding season) (Kendeigh 1969, Mewaldt & King 1978, Helm et al. 2009, Rohwer et al. 2009, Elrod et al. 2011), perhaps more so than phylogenetic relationships (Guallar et al. 2016).

Another interesting finding was the presence of three generations of feathers in a male, as evidenced by the replacement of several tracts of body feathers and the symmetrical replacement (both wings) of the innermost greater covert and the last two tertials (s8, s9), which suggests the presence of a first alternate plumage. All temperate passerines that undergo a first prealternate molt also undergo a definitive prealternate molt (Pyle 1997a, 1997b) and, presumably, this molt exists in *P. bonariensis*. The lack of any other evidence for definitive alternate plumage in *P. bonariensis* may owe in part to the similar brightness of formative feathers and those obtained after subsequent basic molts, which hampered the recognition of replaced feathers from a prealternate molt, in captured individuals and the fading of plumage coloration in museum specimens. To this can be added that the extent of the prealternate molt may vary from absent to limited (Pyle 1997a, 1997b) and this case of partial replacement may represent and unusual extensive pattern. We suggest that it may involve replacement of body feathers but no wing feathers, and first-cycle males may have more extensive prealternate molts than other age-sex groups, as has been observed in some temperate passerines (Pyle 1997a, 1997b).

Previous studies of temperate zone species of North America (Pyle 1997b, Guallar et al. 2009) indicate the presence of prealternate molts that are commonly found in many species of Tyrannidae and Parulidae, whereas in Central and South America, prealternate molt is found in the families Tyrannidae, Tityridae, Emberizidae, and Thraupidae (Ryder & Wolfe 2009, Wolfe et al. 2010, Gómez et al. 2012, Hernández 2012, Moreno-Palacios et al. 2017, Johnson & Wolfe 2018). Furthermore, partial feather replacement is also shared by other Thraupidae spe-

Table 3. Summary of molt patterns of other species of the family Thraupidae studied.

Genus, species, or subspecies	Country of study	Author	Preformative molt	Prealternate molt
Cyanerpes spp.	El Salvador	Dickey & Van Rosen (1838)	Complete	Partial
Tiaris olivaceus	Cuba	Pyle et al. (2004)	Partial	Partial
Phonipara canora	Cuba	Pyle et al. (2004)	Partial	Partial
Ramphocelus bresilius	Brazil	Mallet-Rodrigues (2005)	Complete	Unknown
Tachyphonus spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Partial	Unknown
Ramphocelus nigrogularis	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Incomplete	Unknown
Ramphocelus passerini	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Incomplete	Unknown
Dacnis spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Partial	Unknown
Anisognathus spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Complete	Unknown
Buthraupis spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Complete	Unknown
Tangara spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Partial	Unknown
Thraupis spp.	Costa Rica & Ecuador	Ryder & Wolfe (2009)	Partial	Partial
Sporophila funerea	Costa Rica	Wolfe et al. (2009a)	Partial	Absent
Sporophila corvina	Costa Rica	Wolfe et al. (2009a)	Incomplete-Complete	Limited?
Thraupis episcopus	Costa Rica	Wolfe et al. (2009a)	Partial	Absent
Diglossa albilatera	Colombia	Botero-Delgadillo et al. (2012)	Partial	Absent
Diglossa sittoides	Colombia	Gómez et al. (2012)	Incomplete	Absent
Volatinia jacarina	Colombia	Gómez et al. (2012)	Incomplete	Absent
Tachyphonus rufus	Colombia	Gómez et al. (2012)	Partial	Absent
Tachyphonus luctuosus	Colombia	Gómez et al. (2012)	Partial	Absent
Eucometis penicillata	Colombia	Gómez et al. (2012)	Partial/Incomplete	Absent
Cyanerpes caeruleus	Colombia	Gómez et al. (2012)	Incomplete	Absent
Tersina viridis	Colombia	Gómez et al. (2012)	Partial	Absent
Sporophila angolensis	Colombia	Gómez et al. (2012)	Incomplete	Absent
Sporophila nigricollis	Colombia	Gómez et al. (2012)	Incomplete	Absent
Saltator maximus	Colombia	Gómez et al. (2012)	Incomplete	Absent
Saltator striatipectus	Colombia	Gómez et al. (2012)	Incomplete	Absent
Thlypopsis fulviceps	Colombia	Gómez et al. (2012)	Partial	Absent
Coereba flaveola	Colombia	Gómez et al. (2012)	Partial	Absent
Tiaris obscurus	Colombia	Gómez et al. (2012)	Partial-Incomplete	Absent
Tangara cyanoptera	Colombia	Gómez et al. (2012)	Partial	Absent
Tangara heinei	Colombia	Gómez et al. (2012)	Partial-Incomplete	Absent
Tangara gyrola	Colombia	Gómez et al. (2012)	Partial/Incomplete	Absent
Thraupis episcopus	Colombia	Gómez et al. (2012)	Partial	Absent
Thraupis palmarum	Colombia	Gómez et al. (2012)	Partial	Absent
Tangara vitriolina	Colombia	Hernández (2012)	Partial	Limited/Partial
Tangara arthus	Colombia	Hernández (2012)	Partial	Absent
Sicalis luteola	Chile	Pyle et al. (2015)	Incomplete	Partial
Phrygilus grayi	Chile	Pyle et al. (2015)	Partial	Limited/Partial
Phrygilus fruticeti	Chile	Pyle et al. (2015)	Partial/Incomplete	Absent
Phrygilus alaudinus	Chile	Pyle et al. (2015)	Partial/Incomplete	Limited
Diuca diuca	Chile	Pyle et al. (2015)	Partial/Incomplete	Limited?
Volatinia jacarina	Colombia	Moreno-Palacios et al. (2017)	Complete	Partial
Sporophila intermedia	Colombia	Moreno-Palacios et al. (2017)	Complete	Partial
Chlorophanes spiza spiza	Brazil	Johnson & Wolfe (2018)	Incomplete	Absent
Hemithraupis flavicollis	Brazil	Johnson & Wolfe (2018)	Complete	Limited?-Partial

Table 3. Continuation.

Genus, species, or subspecies	Country of study	Author	Preformative molt	Prealternate molt
Volatinia jacarina jacarina	Brazil	Johnson & Wolfe (2018)	Complete	Partial
Tachyphonus cristatus cristatellus	Brazil	Johnson & Wolfe (2018)	Complete	Absent
Tachyphonus surinamus surinamus	Brazil	Johnson & Wolfe (2018)	Complete	Absent
Ramphocelus carbo carbo	Brazil	Johnson & Wolfe (2018)	Complete	Absent
Lanio fulvus fulvus	Brazil	Johnson & Wolfe (2018)	Complete	Partial
Cyanerpes caeruleus microrynchus	Brazil	Johnson & Wolfe (2018)	Complete?	Limited?/Partial?
Sporophila castaneiventris	Brazil	Johnson & Wolfe (2018)	Complete?	Partial
Sporophila angolensis torrida	Brazil	Johnson & Wolfe (2018)	Complete	Limited?/Partial
Saltator grossus grossus	Brazil	Johnson & Wolfe (2018)	Partial	Absent
Saltator maximus maximus	Brazil	Johnson & Wolfe (2018)	Partial	Absent
Coereba flaveola minima	Brazil	Johnson & Wolfe (2018)	Complete	Absent
Tangara gyrola gyrola	Brazil	Johnson & Wolfe (2018)	Partial?/Incomplete	Absent
Thraupis episcopus	Brazil	Johnson & Wolfe (2018)	Complete	Partial?
Ixothraupis varia	Brazil	Johnson & Wolfe (2018)	Partial?	Unknown
Ixothraupis punctata punctata	Brazil	Johnson & Wolfe (2018)	Partial	Unknown

cies studied in the tropics (Dickey & van Rossem 1938, Ryder & Wolfe 2009, Wolfe et al. 2009b, Pyle et al. 2015, Moreno-Palacios et al. 2017) (Table 3). The presence of prealternate molts in tropical resident species has been suggested to be due prolonged exposure to UV light, and appears to be common in species inhabiting canopy and open areas as grasslands and scrubs (Moreno-Palacios et al. 2017, Johnson & Wolfe 2018), the latter habitats being preferred by *P. bonariensis* in Perú. In addition, replacement of feathers as consequence of prealternate molts may cause changes on feather pigmentation, which might play an important role as a sexual ornament used for mate selection (Searcy & Nowicki 2005, Moreno-Palacios et al. 2017). However, more information is needed to confirm the presence of a first prealternate molt for *P. bonariensis* and to document the presence or absence of prealternate molts in other resident species in the Neotropic (Guallar et al. 2016).

There are other approaches used to determine the age of passerines, such as determining the degree of skull ossification, a procedure widely used on birds worldwide. This criterion becomes a useful tool when the rate and the extent to which the cranium of each species ossifies in relation to maturation and plumage stage are known (Pyle 1997b). We observed that individuals of *P. bonariensis* could complete the ossification process in the preformative molt (Figures 3, 4). This result corroborates what has been suggested for other tanagers in the Neotropics, which may complete skull ossification during or late in the preformative molt (Johnson & Wolfe 2018). In addition, some adults in basic plumage may retain small windows for long periods during the skull ossification process. This phenomenon has also been documented in other groups of Neotropical birds, such as tyrannids, furnariids, and turdids (Pyle 1997b, Pyle et al. 2015). More data should be compiled in order to establish timing for an accurate age determination of *P. bonariensis* based on the completion of skull ossification (Pyle 2015).

The understanding of molt patterns and their timing, and the establishment of aging criteria in the *P. bonariensis* will serve as a framework to aid future studies in population dynamics, natural history, and conservation for this and other species sharing similar ecologies and molt strategies. We encourage bird banders working in the Neotropic to publish their findings that would support or refute findings reported here.

ACKNOWLEDGMENTS

Special thanks to Emil Bautista and Cástulo Obispo, and to the landowners of the community of “San Pedro de Casta” for granting us permission to work on their properties. Thanks to our many volunteers of the “Estación Biológica Río Santa Eulalia” for their assistance during fieldwork; special mention to Maria Antezana, Frank Rodríguez, Giancarlo Guillen, and Raúl Mandujano. This research was conducted under permit RD Nº 213-203-MINAGRI-DGFFS/DGEFFS, Ministerio de Agricultura y Riego, Dirección General Forestal y de Fauna Silvestre. Our thanks to Programa de Anillamiento CORBIDI, led by Eveling Tavera, for providing bands and banding tools for the project. Thanks to Thomas Valqui for the permission and access to specimens housed at Colección Ornitológica John O’Neill. This manuscript was greatly improved by comments provided by Mauricio Ugarte, Ian Ausprey, Felicity Newell, Christopher Kirkby, Kelly Keenan, and Daniel Lane.

Figure 4. Comparison of diagnostic characters for age or sex category for the Blue-and-yellow Tanager (*Pipraeidea bonariensis*) in basic plumage and in formative plumage according to the tabular format of Pyle (1997b) from Sakai & Ralph (2002). Most diagnostic characteristics are listed first in boldface. Age categories with no plumage differences by sex are noted as "Male=Female". Arrow symbols (→) are used on the right side of a particular pair of cells to indicate that the information is carried over from the left side. See text and Table 1 for definitions of molt cycle-based age codes.

DPB (May-Sep)

FPF (Jun-Jan)

Formative and Basic Plumage	DCB Male (Jul-May)	DCB Female (Jul-May)	FCF Male (Jun-Mar)	FCF Female (Jun-Mar)	FCJ Male=Female (May-Sep)
Head color	Bright blue	Grayish with heavy blue wash	Relatively light blue	Grayish with moderate to heavy blue wash	Dull bluish gray
Rump	Bright yellow	Dark yellow	Dark to brightish yellow	Dark yellow	Dark yellowish brown
Molt limit	Uniformly adult	→	**Molt limit** in greater coverts, retained outer coverts relatively abraded & brownish, **contrasting** with fresher black & bluish edged, replaced inner coverts	**Molt limit** in greater coverts but, may also occur between greater coverts and primary coverts contrasting with fresher, blackish, and bluish edged greater coverts	No contrast
Flight feathers (including primary coverts and rectrices)	Uniformly black	Blackish	Dark brown to brown	→	Grayish
Shape of rectrices	Truncate and relatively fresh	→	Tapered, or truncated, or mixed tapered & truncated	→	Tapered
Skull Ossification	Usually ossified, however, some individual may retain small windows (<3mm)	→	Often unossified to nearly ossified, however, some individual may evidence completely ossified skulls.	→	Unossified skull (<1/3 of the skull is ossified)

REFERENCES

Botero-Delgadillo, E, N Bayly & C Gómez-Montes (2012) Ciclos de muda en *Diglossa albilatera* (Thraupidae) y evidencia de un patrón en la adquisición del dicromatismo sexual en el género *Diglossa*. *Boletín de la Revista Científica de la Sociedad Antioqueña de Ornitología* 21: 1–7.

Bridge, ES (2011) Mind the gaps: what is missing in our understanding of feather molt. *The Condor* 113: 1–4.

Burns, KJ (1997) Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. *Molecular phylogenetics and evolution* 8: 334–348.

Burns, KJ, AJ Shultz, PO Title, NA Mason, FK Barker, J Klicka, & IJ Lovette (2014) Phylogenetic and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular phylogenetics and evolution* 75: 41–77.

Dickey, DR & AJ van Rossem (1938) The birds of El Salvador. *Field Museum of Natural History* 23: 1–609.

Dwight, J (1900) The sequence of plumages and molt of the passerine birds of New York. *Annals of the New York Academy of Science* 13:73–360.

Eaton, SW (2001) Pneumatization of the skull in the Parulidae. *The Wilson Journal of* Ornithology 113: 273–278.

Elrod, ML, NE Seavy, RL Cormier & T Gardali (2011) Incidence of eccentric molt in first-year Wrentits increases with fledge date. *Journal of Field Ornithology* 82: 325–332.

Foster, M (1975) The overlap of molting and breeding in some tropical birds. *The Condor* 77: 304–314.

Froehlich, D (2003) *Ageing North American landbirds by molt limits and plumage criteria: a photographic companion guide to the Identification guide to North American birds, Part I*. Slate Creek Press, Bolinas, California, USA.

Gómez, C, E Botero-Delgadillo, NJ Bayly, MI Moreno & CA Páez (2012) Documentando estrategias de muda en aves neotropicales: ejemplos de la Sierra Nevada de Santa Marta, Colombia. *Ornitología Neotropical* 23: 129–138.

Guallar, S, A Ruíz-Sánchez, R Rueda-Hernández & P Pyle (2014) Moult topography and its application to the study of partial wing-moult in two Neotropical wrens. *Ibis* 156: 311–320.

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

Guallar, S, A Ruíz-Sánchez, R Rueda-Hernández & P Pyle (2018) Preformative wing molt in 23 Neotropical resident passerine species. *Ornitología Neotropical* 29, Special Issue: S3–S10.

Guallar, S, E Santana, S Contreras, H Verdugo & A Gallés (2009) Passeriformes del occidente de México: morfometría, datación y sexado. *Instituto de Cultura de Barcelona* 5: 1–458.

Helm, B, I Schwabl & E Gwinner (2009) Circannual basis of geographically distinct bird schedules. *Journal of Experimental Biology*, 212: 1259–1269.

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

Howell, SNG (2010) *Molt in North American birds*. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.

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.

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 (2018) Molt in Neotropical birds: life history and aging criteria. CRC Press, Boca Raton, Florida, 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.

Kendeigh, SC (1969) Energy responses of birds to their thermal environments. *The Wilson Bulletin* 81: 441–449.

Mallet-Rodrigues, F (2005) Molt-breeding cycle in passerines from a foothill forest in southeastern Brazil. *Revista Brasileira de Ornitologia* 13: 155–160.

Marini, MA & R Durães (2001) Annual patterns of molt and reproductive activity of passerines in south-central Brazil. *The Condor* 103: 767–775.

Mewaldt, LR & JR King (1978) Latitudinal variation in post-nuptial molt in Pacific Coast White-crowned Sparrows. *The Auk* 95: 168–174.

MINAM (2012) *Memoria descriptiva del mapa de cobertura vegetal del Perú.* Viceministerio de Desarrollo Estratégico de los Recursos Naturales. Dirección General de Evaluación, Valoración y Financiamiento del Patrimonio Natural. 1ª ed. San Isidro, Lima, Perú.

Moreno-Palacios, M (2013) Patrones de muda de *Volatinia jacarina* y *Sporophila intermedia* (Aves: Thraupidae), en un matorral secundario del bosque seco tropical del departamento de Tolima. M.Sc. thesis, Univ. del Tolima, Ibagué, Colombia.

Moreno-Palacios, M, S Losada-Prado & MA Echeverry-Galvis (2014) Ciclos de reproducción y muda del Volatinero Negro (*Volatinia jacarina*) y el Semillero Gris (*Sporophila intermedia*) en un matorral secundario al norte del Tolima, Colombia. *Ornitología Neotropical* 25: 421–431.

Moreno-Palacios, M, S Losada-Prado & MA Echeverry-Galvis (2017) Secuencia de mudas y plumajes de *Volatinia jacarina* y *Sporophila intermedia* en el valle del Magdalena. *Ornitología Colombiana* 16: eA02.

Mulvihill, RS & RL Winstead (1997) Variation in the extent of the first prebasic wing molt of Dark-eyed Juncos. *Journal of Field Ornithology* 68: 183–199.

North American Banding Council (NABC) (2001) *The North American banders' study guide*. North American Banding Council, Point Reyes Station, California, USA.

Piratelli, AJ, MAC Siqueira & LO Marcondes-Machado (2000) Reprodução e muda de penas em aves de sub-bosque na região leste de Mato Grosso do Sul. *Ararajuba* 8: 99–107.

Poulin, B, G Lefebvre & R McNeil (1992) Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295–2309.

Pyle, P (1997a) Molt limits in North American passerines. *North American Bird Bander* 22: 49–89.

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

Pyle, P (2007) Revision of molt and plumage terminology in ptarmigan (Phasianidae: *Lagopus* spp.) based on evolutionary considerations. *The Auk* 124: 508–514.

Pyle, P & R Kayhart (2010) Replacement of primaries during the prealternate molt of a Yellow Warbler. *North American Bird Bander* 35: 178–181.

Pyle, P, A Engilis & AD Kelt (2015) *Manual for ageing and sexing landbirds of Bosque Fray Jorge National Park and north-central Chile, with notes on occurrence and breeding seasonality.* Special Publication of the Occasional Papers of the Museum of Natural Science, Baton Rouge, Louisiana, USA.

Pyle, P, A McAndrews, P Velez, 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.

Ralph, CJ, KR Hollinger & RI Frey (2012) *Redwood Sciences Laboratory and the Klamath Demographic Monitoring Network mist-netting station management procedures.* U.S. Department of Agriculture, Forest Service Pacific Southwest Research Station Redwood Sciences Laboratory, Arcata, California, USA.

Rohwer, S, RE Ricklefs, VG Rohwer & MM Copple (2009) Allometry of the duration of flight feather molt in birds. *Public Library of Science* 7: e1000132.

Ruíz-Sánchez, A, R Rueda-Hernández, S Guallar & P Pyle (2012) Age determination of the Spot-breasted Wren and the White-breasted Wood-Wren using molt limits. *North American Bird Bander* 37: 93–100.

Ryder, TB & R Durães (2005) It's not easy being green: using molt and morphological criteria to age and sex green-plumage manakins (Aves: Pipridae). *Ornitología Neotropical* 16: 481–491.

Ryder, TB & JD Wolfe (2009) The current state of knowledge on molt and plumage sequences in selected Neotropical bird families: a review. *Ornitología Neotropical* 20: 1–18.

Sakai, WH & CJ Ralph (2002) The tabular format of Pyle's ageing and sexing methods for landbirds. *North American Bird Bander* 27: 77–90.

Schulenberg, TS, DF Stotz, DF Lane, JP O'Neill & TA III Parker (2010) Birds of Peru revised and updated. Princeton Univ. Press, Princeton, New Jersey, USA.

Searcy, WA & S Nowicki (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton Univ. Press, Princeton, New Jersey, USA.

Svensson, L (1992) *Identification guide to European passerines*. 4th ed. L. Svensson, Stockholm, Sweden.

Weisshaupt, N & A Vilches-Morales (2010) Age determination of Corn Buntings *Emberiza calandra* by skull ossification after the autumn moult. *Ringing & Migration* 25: 56–58.

Wolfe, JD & P Pyle (2012) Progress in our understanding of molt patterns in Central American and Caribbean landbirds. *Ornitología Neotropical* 23: 169–176.

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

Wolfe, JD, RB Chandler & DI King (2009b) Molt patterns, age and sex criteria for selected highland Costa Rican resident landbirds. *Ornitología Neotropical* 20: 451–459.

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.