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AGE-BASED PLUMAGE CHANGES IN THE LANCE-TAILED MANAKIN: A TWO-YEAR DELAY IN PLUMAGE MATURATION

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Abstract. I investigated the relationship of plumage to age and sex in the Lance-tailed Manakin (Pipridae, *Chiroxiphia lanceolata*) in the lowlands of western Panama from 1999–2004. I captured birds in mist nets, categorized their plumages, examined them for molt, and followed them for several years to document plumage changes. Male Lance-tailed Manakins exhibited three distinct postjuvenal plumages. Males achieved definitive adult plumage through sequential changes that occurred in the same order as in other *Chiroxiphia* manakins. Definitive male plumage developed over the same time span as reported for *C. caudata* but one year faster than *C. linearis*. Juvenal male plumage was similar to that of females, and 5% of 226 females had plumage similar to formative male plumage. Genetic sexing verified that changes observed late in the formative male plumage unambiguously identified sex and age of individual birds. This information can be used in behavioral studies to identify the age of male Lance-tailed Manakins captured in any of the predefinitive plumage stages.

Key words: Chiroxiphia, *delayed plumage maturation, Lance-tailed Manakin, Panama, plumage development.*

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Cambios de Plumaje Relacionados con la Edad en *Chiroxiphia lanceolata*: Dos Años de Demora en la Maduración del Plumaje

Resumen. Investigué la relación entre el plumaje, la edad y el sexo en *Chiroxiphia lanceolata* (Pipridae) en el oeste de Panamá entre 1999 y 2004. Capturé aves con redes, clasifiqué sus plumajes, examiné la muda del plumaje y los observé durante algunos años para documentar cambios en su plumaje. Los machos presentaron tres plumajes post-juveniles distintos. Los machos alcanzan el plumaje definitivo adulto mediante cambios secuenciales que ocurren en el mismo orden en otros saltarines del género *Chiroxiphia*. El plumaje definitivo se desarrolló en el mismo tiempo que en *C. caudata*, pero un año más rápido que en *C. linearis*. El plumaje de los machos juveniles fue similar al de las hembras, y el 5% de 226 hembras presentó un plumaje parecido al plumaje formativo de los machos. Por medio de análisis genéticos de identificación de sexos, verifiqué que los cambios tardíos observados en el plumaje formativo de los machos permitieron identificar el sexo y la edad de los individuos sin ambigüedades. Esta información puede ser usada en estudios de comportamiento para identificar la edad de los machos con cualquier plumaje predefinitivo.

The Lance-tailed Manakin (*Chiroxiphia lanceolata*) is a small (15.5–22 g), mostly frugivorous passerine in the family Pipridae. This species inhabits lowland forests of southwestern Costa Rica, western Panama, northeastern Columbia, and northern Venezuela and is notable for the elaborate cooperative lek displays of males (Wetmore 1972, Ridgely and Tudor 1994). Like the majority of manakin species, *C. lanceolata* are sexually dimorphic. Adult males have a definitive male plumage of black body feathers with grayish-black rump, blue upper back, and a bright red cap of long narrow feathers. Females are olive-green with paler ventral regions, and some adult females have red or orange crest feathers (Wetmore 1972). Both sexes have bright orange legs, and dark brown or reddish-brown irises, and central rectrices that extend 5–18 mm beyond the length of the other tail feathers.

Young males pass through multiple predefinitive plumages before attaining their definitive adult plumage, but the number of years required for plumage maturation and the reliability of predefinitive plumages in indicating age and sex of individuals is unknown. Research in other *Chiroxiphia* manakins has demonstrated that the time required for plumage maturation varies across species (Foster 1981, McDonald 1993a). Furthermore, the difficulty of distinguishing young males from females has complicated the interpretation of dance displays in which birds that appear to be young males behave like females, or vice versa (Snow 1963, Foster 1981). Here, I describe the complete sequence of plumage changes with age in the Lance-tailed Manakin based on repeated captures of banded individuals over six years. This study is the first to use genetic sexing and recaptures of known-age individuals banded in the nest to confirm the relationship of age and sex to plumage aspect in a *Chiroxiphia* manakin.

METHODS

This study was conducted in a 46-ha area of secondary growth, dry tropical forest on Isla Boca Brava in Chiriquí Province, Republic of Panama (8°12′N, 82°12′W). Postfledging Lance-tailed Manakins were captured using mist nets and individually marked with a numbered aluminum and three colored plastic leg bands. All captured individuals were weighed, measured (tarsus length, unflattened wing chord length, nare to tip of bill, length and width of relaxed crest, tail length, and extension of the longer of the two central rectrices past the main tail), and scored for breeding condition (brood patch or cloacal protuberance). Plumage was categorized based on the color and morphology of crest feathers; presence and extent of black feathers on head, body, wings, and tail; presence and extent of blue feathers on back; and location and extent of growing, sheathed feathers indicative of molt. Limited, asymmetric feather replacement was considered to be adventitious and not part of a molt cycle. Between 1999 and 2004, 457 postfledging individuals were captured on the study site during a total of 2155 mist-net hours (one 12-m net open for one hour). Captures occurred between March and July, a time period that includes the peak of breeding activity at this site (EHD, unpubl. data). An additional 132 individuals were banded as nestlings.

TERMINOLOGY

Molt and plumage terminology follow Humphrey and Parkes (1959) as modified by Howell et al. (2003), with genus-specific classifications analogous to those of McDonald (1993a). I use the term ''predefinitive'' rather than ''subadult'' to denote postjuvenal plumages that change with age, as I have no data on the reproductive competence of young males (Humphrey and Parkes 1959, Foster 1987). Age classes follow Pyle (1997), such that a second-year (SY) bird is in its second calendar year (1 January of the year following fledging through 31 December of the same year). Only physical captures of individuals were considered in constructing the plumage maturation order, as intermediate plumage stages can appear similar when viewed through binoculars under some light conditions. Molt generally began toward the end of the breeding season, so that a male in one subadult plumage during the breeding season of its second year would molt into the next plumage (which it maintained through the breeding season of its third year) while still a second-year bird. Because I observed plumage primarily in the breeding season, I describe plumage-linked age classes as they are observed during the breeding season.

GENETIC SEXING

Because some females have plumage characteristics similar to those of young males, females were identified by the presence of a brood patch or were sexed using molecular techniques. All individuals that had no brood patch when captured in sexually ambiguous plumages were genetically sexed. Individuals captured with black facial plumage or more extensive male plumage characters were assumed to be male, and this was confirmed by genetically sexing 47 individuals in different male plumage categories. DNA was extracted

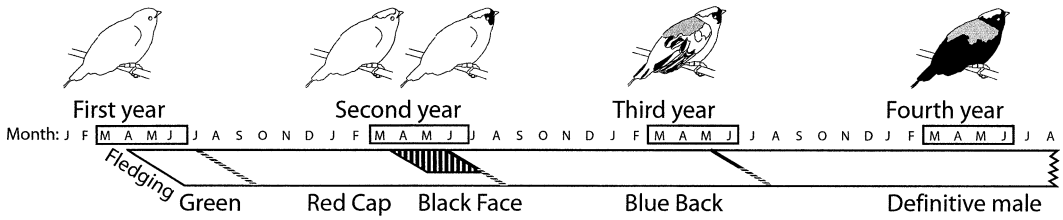

FIGURE 1. Timeline of plumage stages and molt in *Chiroxiphia lanceolata*. Molts are represented by diagonal lines between plumages, corresponding to the range of months in which these molts occurred. Dashed lines indicate estimated time range for molts that were not completely observed due to field season schedules. The cross-hatched portion of the timeline represents the Black Face plumage, which results from a partial molt of facial feathers. Boxed months indicate the beginning and peak of the breeding season, during which most field seasons in this study were conducted.

from whole blood preserved in Longmire's blood buffer solution (Longmire et al. 1988), and sex was determined from a PCR reaction that amplifies the CHD genes on the W and Z chromosomes using primers P2 and P8 (Griffiths et al. 1998). Reaction conditions were as described in Griffiths et al. (1998), using an annealing temperature of 56°C. PCR products were separated by electrophoresis on a 2% agarose gel and stained with ethidium bromide.

STATISTICAL ANALYSES

Measurements for individuals captured more than once in the same year were averaged, and each male was included only once in the measurement data set. For individuals with multiple years of data, I randomly selected one year of data to include. Measurements were not normally distributed and could not be transformed to normality, so I tested for differences among age classes using Kruskall-Wallis tests. When the test indicated significant deviation from the null hypothesis, I tested for significant differences between age categories using Dunn's nonparametric multiple comparisons test for unequal sample sizes (Zar 1999). Data are presented as mean ± one standard deviation.

RESULTS

MOLTING STRATEGY

Lance-tailed Manakins follow a complex basic molt strategy (Howell et al. 2003), with molt and breeding occurring as an annual cycle (Fig. 1). The main molting period begins approximately in June and continues past the end of my field seasons in July. Body feathers of young birds are replaced approximately 2–3 months after fledging in a preformative molt. Feather wear on young birds captured later in their first year suggests that this molt is partial, with remiges and rectrices retained, but the completion of this molt was not observed due to field season schedules. Subsequent ages have complete prebasic molts that begin in June to July of each year. Like other manakins, this species lacks alternate plumages.

MALE PLUMAGE STAGES

Lance-tailed Manakins have definitive adult plumage in the breeding season of their fourth year, after two prebasic molts (Fig. 1, Table 1). Forty-four males were captured at least once while in a predefinitive plumage and again in the consecutive year. Nine of these 44 males were captured in juvenal and both predefinitive plumages. All observed plumage changes by these males agreed with the sequence described below.

Juvenile male Lance-tailed Manakins are green overall, although males may have an orangeish cap of feathers morphologically indistinct from other head feathers (''Tawny Cap'' plumage). The formative male plumage (''Red Cap'') consists of green body feathers, remiges, and rectrices, and a cap of shiny red feathers that are longer and narrower than their other head feathers. This crest initially grows in a ''V'' of two feather tracts along the top of the head that diverge posteriorly, giving the crest a ''split'' appearance. Second-year males attain black lores by the end of the breeding season, with black sometimes extending onto the face (''Black Face'' plumage). The development of Black Face plumage is somewhat variable in timing, but develops after 10–12 months of age. Eleven juvenile males initially captured in Green, Tawny Cap, or slight Red Cap plumage and recaptured in the following year, molted into Red Cap or Black Face plumage in the intervening 8–10 months (mean = 8.7 ± 0.9 months).

The second prebasic molt begins at approximately 13–15 months posthatching. The resulting second basic male plumage (''Blue Back'') comprises a red cap, black face, green-and-black body feathers giving a mottled appearance, scattered blue or partially blue feathers on the back, and variably dark remiges and rectrices. Several of the secondaries or rectrices of these birds are usually black or half black. Twenty-seven males initially captured in Red Cap or Black Face plumage were recaptured in the following year and had molted into Blue Back plumage in the 7.5–13.5 months (mean = 11.3 ± 1.9 months) between captures.

At the third prebasic molt (approximately 26 months posthatching), males attain definitive plumage. Males in their first year of this definitive male adult plumage can have slightly more greenish-black body feathers than males in subsequent years, but these greenish definitive males are indistinguishable from darker males in the field. Sixteen males captured in Blue Back plumage were recaptured in the following year and had molted into definitive male plumage in the 10–14 months (mean = 12.3 ± 1.6 months) between captures.

TABLE 1. Categorization of Lance-tailed Manakin plumages from six years (1999–2004) of field studies in the Republic of Panama. In all, this represents 570 plumage-captures of 467 postfledging individuals.

Plumage[a]	Aspect	Description	Age class[b]	Sex[c]
Juvenal	Green	Olive-green body and flight feathers; may or may not have longer crest feathers, but these are also olive green	HY male/female or AHY female	1 male; 199 females; 13 unknown
	Tawny Cap	Orangeish crest feathers, may or may not be morphologically distinct from other head feathers	HY male or AHY female	8 males; 46 females
Formative	Red Cap	Red, elongated crest feathers; green body and head feathers	SY	56 males; 11 females
	Black Face	Red Cap plumage with some black feathers around lores		45 males; 0 females
Second basic	Blue Back	Red cap, some black on head, scattered blue on back	TY	72 males; 0 females
Third basic	Definitive male	Red cap, black head and body, blue on back	ATY	132 male; 0 females

[a] Plumage terminology follows Humphrey and Parkes (1959). Plumage-type names follow McDonald (1993a).
[b] HY = hatch year; AHY = after hatch year; SY = second year; TY = third year; ATY = after third year. Age classes follow Pyle (1997), such that a SY bird is in its second calendar year.
[c] Numbers indicate unique individuals captured in each plumage class by sex. Individuals captured in more than one plumage are counted in each observed plumage stage. Sex was determined as described in methods. All Tawny Cap males were genetically sexed, and five of these eight males were additionally sighted in a later male plumage. Thirteen green-plumaged birds of unknown sex were not genetically sexed.

CAPTURES OF KNOWN-AGE INDIVIDUALS

This general plumage sequence is further confirmed by captures of twelve male chicks banded in the nest that were later captured one or more times in mist nets, providing information on plumage stage for males of precisely known age (Table 2). One of these males was captured at two months of age with Tawny Cap plumage; one male captured at nine months of age had Red Cap plumage, with the cap incomplete in ''split'' formation; seven males captured at 10–12 months of age were in Black Face plumage; two males captured at 12–13 months of age showed small amounts of blue feathers on the back; four males captured at 24.5–25.5 months had typical Blue Back plumage; and one male captured at 35 months was in full definitive male plumage. The plumage stages of these known-age birds were consistent with the general order and progression of plumages in other young males.

VARIATION IN FEMALE PLUMAGE

Young female Lance-tailed Manakins retain uniformly green plumage after the preformative molt, and this is the definitive plumage of most females. The majority of females (78% of 226 individuals) had completely green plumage as described in Wetmore (1972). A small proportion of individual females had male-like plumage, as reported in some other manakin species (Foster 1981). Approximately 5% of all females had Red Cap plumage, and an additional 17% of females had Tawny Cap plumage. Tawny Cap birds frequently had only a few orangeish feathers in their crests, and were usually classed as green-plumage when sighted with binoculars. The majority of females did not change plumage type between years, but two females initially captured with slight Tawny Cap plumage gradually developed full red crests over two to three breeding seasons. The actual age of females was generally unknown, as most were captured as unbanded immigrants from outside of the field site. Three females banded as chicks were recaptured on the study site, and had completely green plumage at 12.5–13 months of age.

GENETIC SEX BY PLUMAGE TYPE

Genetic sexing of 47 individuals in Black Face or later male plumage confirmed that all were male (9 Black Face, 14 Blue Back, and 24 definitive male). The genetic sex of birds in Green, Red Cap, and Tawny Cap plumage was examined on a per-capture basis, as males were frequently recaptured in later plumage stages. Females represented 16.4% of 67 Red Cap captures, 85% of 54 Tawny Cap captures, and 99.5% of 213 birds in Green plumage (Table 1).

CHANGES IN PLUMAGE MORPHOLOGY WITH AGE

Several changes in plumage morphology were linked with age in young males. I examined differences in plumage characteristics of known-age birds aged by capture in predefinitive plumage and found that the length of r1 (the longest extended middle rectrix) was significantly different among age classes ($df = 3$, $Z = 63.3$, $P \leq 0.001$), as were the area of the red crest ($df = 2$, $Z = 26.8$, $P \leq 0.001$) and wing chord length ($df = 3$, $Z = 66.0$, $P \leq 0.001$; Fig. 2). Multiple comparisons indicated that third- and fourth-year males were significantly different from younger birds in wing

TABLE 2. Plumage stage of 12 males banded in the nest and later recaptured.

Individual	Hatch date	Recapture date	Age (months)	Plumage at recapture[a]
248	18 Apr 2000	26 Mar 2001	11	BF (slight)
		28 Apr 2001	12	BF (slight)
249	18 Apr 2000	31 May 2002	25.5	BB
		06 Jun 2002	25.5	BB
283	05 May 2000	10 Apr 2001	11	BF (slight)
		23 Apr 2001	11.5	BF
		26 Apr 2002	23.5	BB
		19 May 2002	24	BB
287	10 May 2000	26 Mar 2001	10	BF (slight)
		07 May 2001	12	BB (slight)
		17 Jun 2001	13	BB (slight)
302	23 May 2000	22 Jun 2001	13	BB
		30 May 2002	24	BB
374	20 Apr 2001	21 Jun 2001	2	TC
		25 Jun 2001	2	TC
403	06 May 2001	03 Apr 2004	35	DM
422	26 Apr 2001	27 Apr 2002	12	BF (slight)
444	13 Jun 2001	26 Mar 2002	9	RC (split)
466	10 Apr 2002	09 Apr 2003	12	BF (slight)
		29 Apr 2003	12.5	BF (slight)
		03 Apr 2004	24	BB
535	16 Jun 2002	08 Apr 2003	10	BF
546	17 Jun 2002	10 Apr 2003	10	BF (slight)

[a] Plumage-stage codes are as follows: BF = Black Face, BB = Blue Back, TC = Tawny Cap, DM = Definitive male, and RC = Red Cap. ''Slight'' indicates plumage which meets the plumage stage definitions in Table 1 but which may be mistaken for the previous plumage when viewed with binoculars. ''Split'' indicates a V-shaped, developing red cap with feathers emerged in two distinct tracts on the head.

chord and cap area ($P \leq 0.05$ indicated by $Q_{0.05,5} > 2.8$), but not different from each other. Third- and fourth-year males were different from each other and from younger birds in tail extension length (Fig. 2).

DISCUSSION

Predefinitive male plumages in the Lance-tailed Manakin are reliable indicators of age for second-year (Red Cap or Black Face) and third-year (Blue Back) males. Furthermore, individuals in Black Face and later plumages are unambiguously male. The majority of females have all-green plumage, although some have orangeish or red caps indistinguishable from those of hatch-year or second-year males.

Throughout the genus *Chiroxiphia*, the acquisition of adult male plumage elements occurs in the same general order: males start with a green base plumage; then gain a cap of elongated red feathers; next black feathers on the face or lores; then blue back feathers and some black body, tail and flight feathers; and finally replace remaining green with black or blue feathers (Foster 1987, McDonald 1993a). The timing of molts and overall length of time to attain adult male plumage in *C. lanceolata* is more similar to *C. caudata* (Foster 1987) than to *C. linearis* (McDonald 1989). Male *C. caudata* (Foster 1987) and *C. lanceolata* attain definitive plumage by the breeding season of their fourth year, while *C. linearis* attain definitive adult plumage by their fifth year (Foster 1977, Foster 1987, McDonald 1993a). The timing of the Red Cap, Black Face, and Blue Back plumage stages in *C. linearis* is debated. Foster (1987) reported that the Red Cap and Black Face stages occur in only one year class (second-year), and she separated Blue Back males into two year stages (third- and fourth-year). McDonald (1993a) divided Red Cap and Black Face males into two age classes (second- and third-year), but combined all Blue Back males in one age class (fourth-year). This study demonstrates that in *C. lanceolata*, the Red Cap and Black Face plumages are included within one age class and molt stage, as reported for *C. caudata*. Also as in *C. caudata*, Blue Back males in *C. lanceolata* are defined by one molt and age class, though the extent of blue on the back and the degree of dark body feathers and remiges varies by individual and may change during a protracted molt.

Species-level differences in delayed plumage maturation may be related to differences in the time required to attain a breeding position (Foster 1987, McDonald 1993b). Only males of alpha or beta status perform courtship displays for females (McDonald 1989), and alpha and beta males in *C. linearis* are usually at least 8 years old (McDonald 1993b). In contrast, male *C. lanceolata* may become betas at 4 or 5 years of age (EHD, unpubl. data).

My results demonstrate that the plumage of young male Lance-tailed Manakins may be used to estimate reliably the age of individuals captured in any of the distinct predefinitive plumage classes. This is of particular utility in long-term studies of banded individuals, as plumage can be used to determine accurately the age of adult males previously captured in predefinitive plumages.

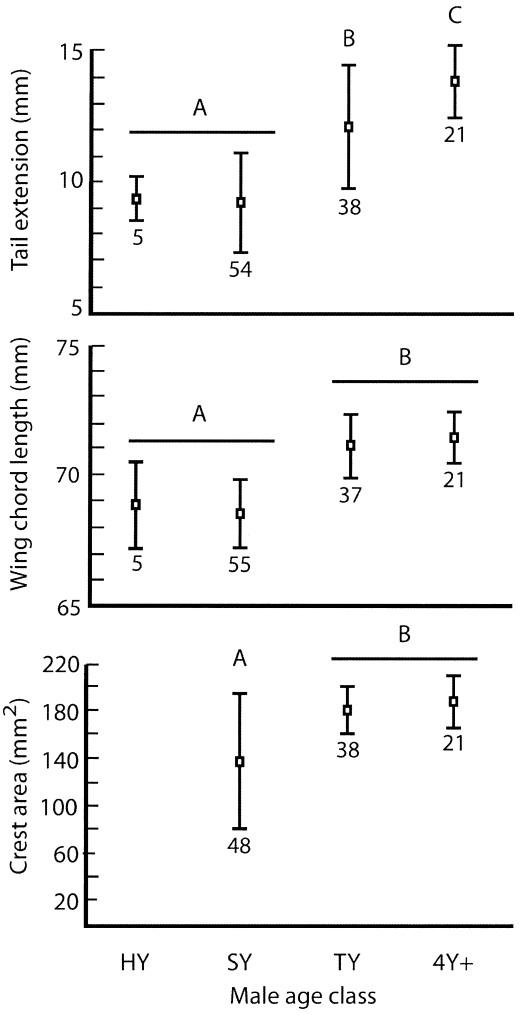

FIGURE 2. Differences in male plumage morphology by age class. Hatch-year and second year males have shorter central rectrices and wing chord lengths than males in their third year or older. Second-year males also have significantly smaller crest areas than older males. Letter codes indicate that groups differed significantly ($P \leq 0.05$, Dunn's nonparametric multiple comparisons test for unequal sample sizes, Zar 1999). Codes for age classes refer to Table 1. Graphs represent mean (± SD) of plumage measurements with sample sizes shown below each bar. Males of known age in their fourth ($n = 15$) and fifth ($n = 6$) years were pooled into one age class, 4Y+.

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