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PLUMAGE DEVELOPMENT AND MOLT IN LONG-TAILED MANAKINS (*CHIROXIPHIA LINEARIS*): VARIATION ACCORDING TO SEX AND AGE

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ABSTRACT.—Lek-mating Long-tailed Manakins (*Chiroxiphia linearis*) exhibit an unusual pattern of delayed plumage maturation. Each year, males progress through a series of predefinitive plumages before attaining definitive plumage in their fifth calendar year. Females also exhibit variation in plumage coloration, with some females displaying male-like plumage characteristics. Using data from mist-net captures in northwest Costa Rica ($n = 1,315$) and museum specimens from throughout the range of Long-tailed Manakins ($n = 585$), we documented the plumage sequence progression of males, explored variation in female plumage, and described the timing of molt in this species. Males progressed through a series of age-specific predefinitive plumages, which enabled the accurate aging of predefinitive-plumaged males in the field; this predefinitive plumage sequence is the basis for age-related status-signaling in these males. Females tended to acquire red coloration in the crown as they aged. However, colorful plumage in females may be a byproduct of selection on bright male plumage. Females exhibited an early peak of molt activity from February to April, little molt from May through July, and a second, more pronounced peak of molt activity in October. By contrast, males in older predefinitive-plumage stages and males in definitive plumage exhibited comparable unimodal distributions in molt activity beginning in June and peaking between July and October. Our data are consistent with selective pressure to avoid the costs of molt–breeding overlap in females and older males. Our findings have important implications for social organization and signaling in Long-tailed Manakins, and for the evolution of delayed plumage maturation in birds. Received 20 May 2005, accepted 5 January 2006.

Key words: *Chiroxiphia linearis*, cooperation, delayed plumage maturation, hierarchy, leks, Long-tailed Manakin, plumage coloration.

Desarrollo del Plumaje y Muda en *Chiroxiphia linearis*: Variación de Acuerdo al Sexo y la Edad

RESUMEN.—En *Chiroxiphia linearis* se presenta un patrón inusual de maduración retardada del plumaje. Cada año, los machos pasan por una serie de plumajes predefinitivos antes de alcanzar su plumaje definitivo en su quinto año calendario. Las hembras también exhiben variación en la coloración del plumaje: algunas presentan características del plumaje similares a las de los machos. Empleando datos de capturas

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hechas con redes de niebla en el noroeste de Costa Rica ($n = 1,315$) y especímenes de museo de todo el rango de distribución ($n = 585$), documentamos la secuencia de plumajes progresivos de los machos, exploramos la variación en el plumaje de las hembras y describimos el momento en que tiene lugar la muda en *C. linearis*. Los machos progresaron a través de una serie de plumajes pre-definitivos específicos para cada clase de edad, lo que permitió determinar la edad de los machos sin plumaje definitivo con exactitud en el campo. Esta secuencia de plumajes predefinitivos es la base para la señalización del estatus entre los machos, que está relacionada con la edad en esta especie. Las hembras tendieron a adquirir coloración roja en la corona a medida que envejecieron. Sin embargo, el plumaje colorido en las hembras podría ser un subproducto de la selección por plumaje brillante en los machos. Las hembras exhibieron un pico temprano de actividad de muda entre febrero y abril, poca muda entre mayo y julio y un segundo pico más pronunciado de actividad de muda en octubre. En contraste, los machos en estadios de plumaje predefinitivo más avanzados y en plumaje definitivo exhibieron distribuciones unimodales de actividad de muda comparables comenzando en junio, con un pico entre julio y octubre. Nuestros datos concuerdan con la existencia de una presión selectiva para evitar los costos del solapamiento de la muda de las hembras y de los machos más viejos. Nuestros hallazgos tienen implicaciones importantes relacionadas con la organización social y la señalización entre individuos de *C. linearis*, y también para la evolución de la maduración retardada del plumaje en las aves.

IN MANY BIRDS, males do not assume definitive, adult-like plumage for one or more years after hatching. In some species, this delay in plumage maturation is accompanied by a delay in sexual maturation (Lawton and Lawton 1986). In many sexually dichromatic, north-temperate passerines, however, males do not attain their definitive plumage until after their first potential breeding season, despite having reached sexual maturity (Rohwer et al. 1980, Lyon and Montgomerie 1986). The adaptive significance of this type of delayed plumage maturation has been the focus of extensive research in recent decades (e.g., Rohwer et al. 1980, Lyon and Montgomerie 1986, Hill 1996), with most studies investigating the one-year delays typically exhibited by north-temperate passerines. However, many tropical passerines deviate from this pattern. In some species, such as bowerbirds and birds of paradise, males molt into the same predefinitive plumage for several years before assuming definitive plumage (Frith and Beehler 1998, Frith and Frith 2004). In other species, for example manakins, Darwin's finches, paradise flycatchers, Hawaiian honeycreepers, and monarch flycatchers, males progress through a transitional series of different predefinitive plumage stages before assuming definitive plumage (Foster 1987; McDonald 1989a, 1993a; Lepson and Freed

1995; VanderWerf 2001; Mulder et al. 2002; DuVal 2005). Investigations of the adaptive significance of delayed plumage maturation, and of the signal function of variation in plumage, require a thorough understanding of plumage development and molt. Here, we investigate age- and sex-related plumage variation in the Long-tailed Manakin (*Chiroxiphia linearis*).

Long-tailed Manakins have a lek-based mating system (Foster 1977; McDonald 1989a, b). Males gather at lek sites, where they establish age-graded dominance hierarchies. The two most dominant males at each lek, the alpha and beta males, perform vocal duets and elaborate, dual-male dance displays for females visiting the leks. Females usually copulate only with alpha males (Foster 1977, McDonald 1989b, McDonald and Potts 1994). As in other lekking species (Höglund and Alatalo 1995), females are solely responsible for rearing offspring (Foster 1976).

As they grow older, male Long-tailed Manakins progress through a series of transitional, predefinitive plumage stages before attaining definitive plumage in their fifth calendar year (Foster 1987; McDonald 1989a, 1993a). This delay is unusually long for such a small (15–21 g) passerine (Lawton and Lawton 1986). Female Long-tailed Manakins also vary in plumage color, with some females developing red or tawny crown feathers, a trait believed

to be associated with age (McDonald 1989b). Such extensive age- and sex-based variation in plumage may present unique signaling opportunities, particularly in species with complex social organization (Lawton and Lawton 1986). In Long-tailed Manakins, for example, a male's position within a lek hierarchy may be largely influenced by his age. Thus, transitional plumages that reliably signal a male's age or status in the hierarchy would likely reduce the occurrence of costly, escalated encounters between males of low and high status (Foster 1987, McDonald 1993a).

Foster (1987) described predefinitive male plumages in Long-tailed Manakins as transitioning through several stages along a continuous spectrum, with second-year males being mostly green with a red crown patch and, occasionally, some black on the face, coverts, and body and flight feathers, and third- and fourth-year males having a mixture of red, green, black, and blue plumage. McDonald (1989a, 1993a) proposed an alternative sequence, whereby males progress through a transitional series of age-specific predefinitive plumages; in this proposed sequence, males develop a red crown in their second year, a black mask in their third year, and a blue mantle in their fourth year. Using recapture and resighting data from three study populations, together spanning 27 years, we re-examined the plumage sequences proposed by Foster (1987) and McDonald (1989a, 1993a) to determine whether predefinitive male plumage can reliably signal age in Long-tailed Manakins. Additionally, we investigated patterns of variation in female plumage and described sex- and age-based variation in the timing of molt.

METHODS

We studied Long-tailed Manakins at three sites in northwestern Costa Rica: from 1971 to 1974 and in 1977 at the Enrique Jiménez Nuñez Experiment Station (10°20'N, 85°8'W); from 1981 to 1999 in Monteverde (10°18'N, 84°48'W); and from 2003 to 2005, as well as for a few weeks in 1986, in Santa Rosa National Park, Guanacaste Conservation Area (10°40'N, 85°30'W). The Monteverde site is located in premontane tropical moist forest (Holdridge 1966), and the Santa Rosa and Jiménez Station sites encompass both evergreen bottomland moist forest and areas of tropical dry forest on surrounding hillsides

(Stiles and Skutch 1989). All three sites exhibit marked seasonality, with a dry season extending from approximately January through April, and a rainy season extending from May through December. Male Long-tailed Manakins display actively from February through September, with a pronounced peak in activity from March through June (Foster 1977; McDonald 1989a, b, 1993b). Active nests have been discovered from March to July (Foster 1976; S. M. Doucet unpubl. data), though the nesting season likely extends until September (Foster 1976).

We captured 1,315 Long-tailed Manakins using mist nets and fitted each individual with a unique combination of plastic colored leg bands; birds at Monteverde and Santa Rosa also carried a numbered aluminum leg band. Of 20 birds banded as nestlings, only 2 were recaptured or resighted in following years (one male and one female). To determine the plumage sequence followed by birds as they aged, we recorded detailed descriptions of each bird's plumage coloration each time it was captured. Whenever possible, we also recorded plumage descriptions of marked individuals seen during behavioral observations at lek sites or encountered opportunistically at the study sites. Over the course of the study, R.P.C. and M.S.F. noted that second-year birds of both sexes could be identified by the presence of retained juvenal wing feathers; R.P.C. also discovered that the mouth-lining color of second-year birds was diagnostic (Clay 2001). Thus, we examined the mouth-lining color and the amount of wear on wing feathers of all green-plumaged birds captured from 1997 to 1999 and in 2005. Only a subset of the data we present here was described briefly elsewhere (plumage sequence information from 56 males; McDonald 1989a, 1993a).

To assess the timing of molt, we examined all birds captured from 1971 to 1977, some birds captured in 1986 and 1987, and all birds captured since 1995 for signs of molt (i.e., sheathed feathers), recording whether birds were molting at time of capture and noting in which regions of which feather tracts they were molting. Occasionally, we noted extremely asymmetric molt or molt of only a single, isolated feather on some individuals. We assumed in both instances that the molt was adventitious and did not include these individuals in our calculations of proportions of birds molting (Pyle 1997, VanderWerf 2001). Although most birds were

captured and observed between March and July, we collected molt information on wild birds in all months except September and February.

To obtain additional molt data spanning the calendar year, we also examined 585 Long-tailed Manakin specimens in museum collections (see Acknowledgments). We recorded feather regions and tracts with molting feathers and, if discernible, the plumages from which and into which a bird was molting. Many museum specimens were also examined for the presence of juvenal remiges and coverts. Taken together, our data from museum specimens and wild birds spanned the calendar year, though some months are considerably better represented than others. Molt and plumage terminology follow the Humphrey-Parkes (H-P) system (Humphrey and Parkes 1959) as summarized in Pyle (1997). A recent review (Howell et al. 2003) recommends modifications to H-P terminology. The complex nature of molt in Long-tailed Manakins, however, makes it difficult to assign consistent molt terminology to different sex and age classes under the proposed changes. Thus, for simplicity, we opted for traditional H-P terminology. We also follow Pyle's (1997) age terminology. Thus, a hatch-year is a bird in its first calendar year (until 31 December of the year it fledged), a second-year bird is in its second calendar year (from 1 January to 31 December of the year following fledging), a third-year bird is a bird in its third calendar year, and so on.

Wild birds in all-green or primarily green plumage were identified as females if they had a vascularized brood patch, were recaptured or resighted in green plumage in multiple years, were aged as after-second-year birds on the basis of the absence of retained juvenal wing feathers (see above), exhibited female-like behavior during dance displays by males (McDonald 1989a), or were identified as such either by genetic sexing (Griffiths et al. 1998) or by laparotomy. Birds in green plumage were identified as males if they were recaptured or resighted in predefinitive or definitive male plumages in subsequent years or by laparotomy. For museum specimens, green birds were identified as females or males only if the specimen tag indicated the presence of ovaries or testes, respectively. Birds in green plumage that did not meet these criteria were considered of unknown sex and were not included in our analyses.

RESULTS

Molt.—All Long-tailed Manakins underwent a prebasic (postbreeding) molt each year. The olive-green juvenal plumage grown in the nest was identical in males and females. The first prebasic molt began within four months of fledging and was a partial molt: hatch-year birds of both sexes retained some of their juvenal wing feathers. Thus, second-year birds had two generations of wing feathers: retained juvenal remiges and distal greater coverts, and new lesser and median coverts and proximal greater coverts. Additionally, the mouth linings of second-year birds were bright orange to orange-yellow, similar to those of nestlings (Foster 1976), whereas the mouth linings of older birds were paler and more pinkish in color. All subsequent prebasic molts were complete.

Male plumage sequence.—Overall, we captured and marked 653 individuals in Monteverde, 280 individuals at the Jiménez Station, and 382 individuals in Santa Rosa. Many of these birds were recaptured or resighted in one or more subsequent years, which allowed us to document 562 plumage transitions from a total of 235 males. Of these transitions, 343 were successive molts in definitive plumage, whereas 219 were molts from one predefinitive plumage to another or from predefinitive to definitive plumage. Of these 219 informative transitions, we have records for two different plumage stages for 98 males, three different plumage stages for 32 males, and four different plumage stages for 19 males. One male was sighted in all five plumage stages.

Males progressed through the following plumage sequence (Fig. 1 and Tables 1 and 2). They acquired their juvenal plumage in the nest, which, like the plumage of females, was olive green above with a paler wash below. Within four months of fledging, males initiated their first prebasic molt. Males in their first basic plumage, which we term "red-cap plumage," were olive green throughout with a small red crown patch. The amount of red in the crown was highly variable, and males often had two strips of red feathers on the outer edges of the crown rather than a contiguous red crown patch (Fig. 2A). A limited number of males in red-cap plumage also had some black feathers on the face. These black feathers, or additional ones, were acquired along with an expanded red crown in some males during a partial molt (either a limited prealternate

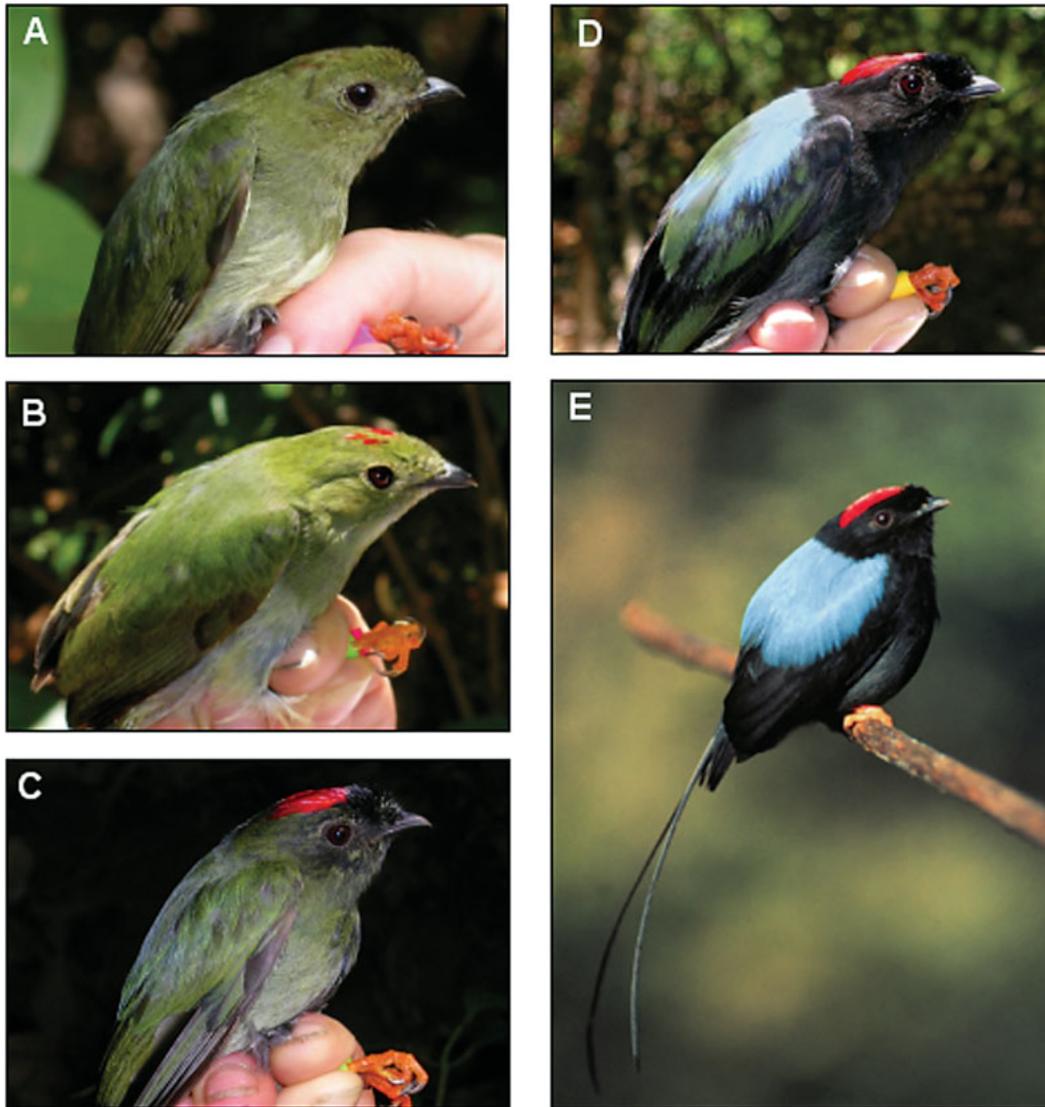


FIG. 1. Typical appearance of birds in different plumage stages: (A) female or male in juvenal plumage, (B) male in red-cap plumage, (C) male in black-face plumage, (D) male in blue-back plumage, and (E) male in definitive plumage. Photograph (E) courtesy of Richard Laval.

molt or the early onset of the second prebasic molt; see below) in March and April. In addition, some males undergoing the first prebasic molt replaced their central, but no other, rectrices (M. S. Foster unpubl. data). These rectrices were darker and longer than those retained from the juvenal plumage.

In the following year, males underwent their second prebasic molt. Males in their second basic plumage, which we term "black-face

plumage," were mostly olive-green with a small red crown patch and a black facial mask or hood. In this plumage, the red crown patch was always contiguous and was larger than that of red-cap males but smaller than that of males in definitive plumage. The amount of black on the face varied from a small black facial mask to a full black hood. Some black-face males also had some black in their coverts and flight feathers, and a blackish tinge to their body plumage.

TABLE 1. Plumage development in male Long-tailed Manakins. Plumage descriptions summarize the typical appearance of males in each plumage stage.

Age range ^a	Age name ^b	Plumage stage	Name of plumage stage	Plumage description
0–4	hatch-year	juvenal	juvenal	Olive green throughout with paler wash below
4–15	second-year	first basic	red-cap	Olive green body and flight feathers; partial red crown
15–27	third-year	second basic	black-face	Olive green body and flight feathers; small red crown; black face or hood
27–39	fourth-year	third basic	blue-back	Black and green body and flight feathers; red crown; blue and green mantle
≥39	≥ fifth-year	definitive-basic	definitive	Black body and flight feathers; red crown; blue mantle

^aMonths since hatching.

^bCalendar year; age terminology follows Pyle (1997); see text for explanation.

TABLE 2. Summary of sequential plumage transitions recorded in male Long-tailed Manakins.

Plumage transitions	Recorded instances (<i>n</i>)
Typical	
Green to red-cap	1
Red-cap to black-face	60
Black-face to blue-back	60
Blue-back to definitive	48
Definitive to definitive	343
Potential anomalies	
Green to black-face	2
Red-cap to blue-back	2

Rarely, males in black-face plumage had a limited number of blue feathers on their mantle.

Males in their third basic plumage, which we term “blue-back plumage,” had a mixture of green and black body and flight feathers, a full red crown patch, and some blue feathers on the mantle. Birds in blue-back plumage exhibited the greatest range of variation in proportions of plumage colors, though all exhibited some blue in the back, and some black ventrally. Often, blue-back males had body feathers that were mostly black with a tinge of olive-green and flight feathers that were black with green edging. Some blue-back males had very little green at all in their plumage and might be mistaken for definitive-plumaged males in the field. Other blue-back males had substantial amounts of green in their black body plumage, giving them an almost grayish appearance.



FIG. 2. (A) A young male Long-tailed Manakin in red-cap plumage and (B) a female Long-tailed Manakin with some partly red crown feathers. Note differences in the distribution of red on the crown, the distribution of red on individual feathers, and the length of red crown feathers.

Finally, males in definitive-basic plumage had entirely jet-black body and flight feathers, a sky-blue mantle, and a bifid, red crown patch. A small number of males molting from blue-black plumage to definitive plumage retained minimal amounts of green on the rump, flanks, or undertail coverts. This green disappeared during the following prebasic molt.

Four lines of evidence allow us to assign ages to these sequences. First, one male banded as a nestling was recaptured or observed in three subsequent years: in his first prebasic molt, he acquired the red-cap plumage; in his second prebasic molt, the black-face plumage; and in his third prebasic molt, the blue-back plumage. (Unfortunately, this male was not resighted again until his sixth calendar year, when he was in definitive plumage.) Second, all red-cap males captured between 1997 and 1999 at Monteverde (32 individuals) and in 2005 at Santa Rosa (11 individuals) were identified as second-year birds on the basis of retained juvenal remiges and distal greater coverts and mouth lining color. Third, we documented the full, four-year progression of 17 males from red-cap plumage to definitive plumage. Finally, all males observed in red-cap plumage invariably had black feathers on the face in the following year. Similarly, all males observed in black-face plumage had blue feathers on their mantle the following year. No male observed in definitive plumage was ever observed to have green feathers in subsequent years. Our observations suggest that this plumage sequence is unidirectional, nonreversible, and remarkably age-specific.

Of the 562 plumage transitions we recorded, 465 were sequential (i.e., the males were recaptured or resighted in the following year). These sequential transitions allowed us to assess the frequency of unexpected plumage transitions. We documented only four unusual plumage transitions. Two males were first captured in all-green plumage and both were recaptured in black-face plumage the following year (Table 2). Because these males were captured in March and April as green males but in the following breeding season as black-face males, it is possible that they showed red in the crown during some of the interval between these records. A third otherwise all-green male was molting in a limited black mask and red crown when it was captured in April. A year later, after a single prebasic molt, it was in blue-back plumage. A fourth presumably

aberrant bird, captured in red-cap plumage and without any black on its body, had a larger red crown, a well-developed black hood (but no other black body feathers), and a small area of blue feathers on the back the following year. Thus, $\leq 0.7\%$ of plumage transitions deviated from the expected pattern. Even if we exclude transitions between definitive plumage stages, these anomalies account for only 1.8% of plumage transitions. These anomalies invariably involved an accelerated plumage-maturation process, because no male ever remained in the same plumage stage for two subsequent years. In 96 instances, more than one year elapsed between recaptures or resightings of particular males. Even among these nonsequential transitions, males were always in the expected plumage category when they were eventually recaptured or resighted, as estimated from the number of years separating recaptures or resightings.

Female plumage.—Female Long-tailed Manakins are typically olive-green above with a paler wash below. However, of the 649 confirmed females examined (including museum specimens), 145 (23%) had variable amounts of tawny or red feathers on the crown, ranging from a single feather to a full tawny or red crown. The presence of red in the crown of females may make it difficult for inexperienced observers to differentiate them from young males in red-cap plumage. However, the red crown feathers of females can be distinguished from those of males by one or more of the following characteristics (Fig. 2). First, the red feathers of females often had a tawny or rusty appearance, a feature never observed in males. Second, the red color was often present on only some of the barbs of each feather in females, while the remainder of the feather remained green, thereby creating a slightly streaked appearance (Fig. 2A). By contrast, the red feathers of young males usually had red distal barbs, and red, orange, or yellow central and proximal barbs, regardless of the number of red feathers on the crown (Fig. 2B). Third, the red feathers of females were usually the same length as the other (green) feathers on the crown, whereas the red feathers of males were usually longer than the green feathers and tended to increase in length with age (Fig. 2; S. M. Doucet pers. obs.). Fourth, the distribution of red feathers on the crown differed between females and males. In females, red feathers could be found in the front, center, or rear of the crown. By

contrast, among males in red-cap plumage, the red feathers tended to grow on the outer edges of the crown, often resulting in a split, rather than contiguous, red crown (Fig. 2A).

Development of tawny coloration in the crown of females appeared to be associated with age. Of the females we were able to age as second-year or after-second-year (on the basis of plumage and mouth lining color), none of 43 second-year females had any trace of red or tawny on the crown, whereas 91 of 189 after-second-year females had traces of tawny or red (Fisher's exact test, $P < 0.00001$). Of the females that exhibited changes in plumage color during the course of the study, nine were observed or recaptured sufficiently frequently to estimate the minimum amount of time elapsed between when the bird was originally captured and when a change in plumage was first noted (mean \pm SD = 5.1 ± 1.17 years). Two of these females were first captured as second-year females; one of these developed a tawny crown in her eighth year, and the other developed red crown feathers in her ninth year. Some females never developed red or tawny crowns, including the three oldest, minimum-age females. Two were recaptured in completely green plumage 10 years after initial capture. A third female, last observed 15 years after her initial capture, had no discernible red or tawny in her crown.

In rarer instances, females departed from the typical olive-green plumage in other ways. During the course of our study, we captured a few females with black lores or black forehead, cheek, or nape feathers ($n = 21$); with one or more partially or completely black wing or tail feathers ($n = 11$); or with blue or black wing or tail coverts or blue mantle feathers ($n = 5$). Apart from crown color, none of these patches was extensive enough to be seen easily in the field. Females with some tawny or red coloration in the crown were significantly more likely to show these additional male-like plumage tendencies (28 of 147) than females that were otherwise all green (6 of 504; Fisher's exact test, $P < 0.00001$). Two of the females that had black or blue on the body were recaptured in subsequent years and no longer had black or blue in their plumage. By contrast, all females with a red or tawny crown that were recaptured in subsequent years retained a colored crown.

Timing of molt.—Long-tailed Manakins follow a complex pattern of molt that varies by age and sex. Among females, there is a bimodal

distribution of the proportion of birds molting over the course of the year, with an early peak of molt activity in March and a second peak in October (Fig. 3A). The molt occurring between February and April is limited to some head and body feathers, whereas the second peak corresponds to the complete prebasic molt. The early peak varies by age. Of the females examined in March and April that we were able to age ($n = 81$), 13 of 15 (86%) second-year females showed signs of molt, whereas only 25 of 66 (38%) after-second-year females showed signs of molt (Fisher's exact test, $P = 0.0003$). Unfortunately, our data do not allow us to determine whether this early peak corresponds to a limited prealternate molt or whether it is an early beginning to the prebasic molt that is suspended through the reproductive period. This distinction would require confirmation that newly molted feathers were replaced in the subsequent prebasic molt (in the case of a limited prealternate molt) or not replaced in the subsequent molt (in the case of an early suspended prebasic molt).

The molt activity patterns of males in predefinitive plumage are more complex. We separated males by plumage stage, which generally corresponds to age (see Table 1, and above). As with females, a large proportion of red-cap (second-year) males showed signs of molt in March and April (Fig. 3B). Among these young males, there was a slight decrease in molt activity in May. By July, however, all red-cap males captured or examined showed signs of molt. Of the red-cap males showing signs of molt in March and April ($n = 28$), 82% were molting only crown or head feathers. Three of these males (11%) were molting both head and body feathers, and two others (7%) were molting only body feathers. Many of these red-cap males were molting in additional red crown feathers and some were molting in black feathers on other parts of the head. In some cases, however, these males were simply molting in green crown or head feathers. The peak of molt in June corresponds to the complete first prebasic molt: males were in a much heavier molt that often included flight feathers. Among black-face (third-year) and blue-back (fourth-year) males, we detected molt in only a small percentage of males (13%) in March and April (Fig. 3C, D). As with red-cap males, this early molt in black-face and blue-back males was largely restricted to the crown and head regions. Black-face and blue-back

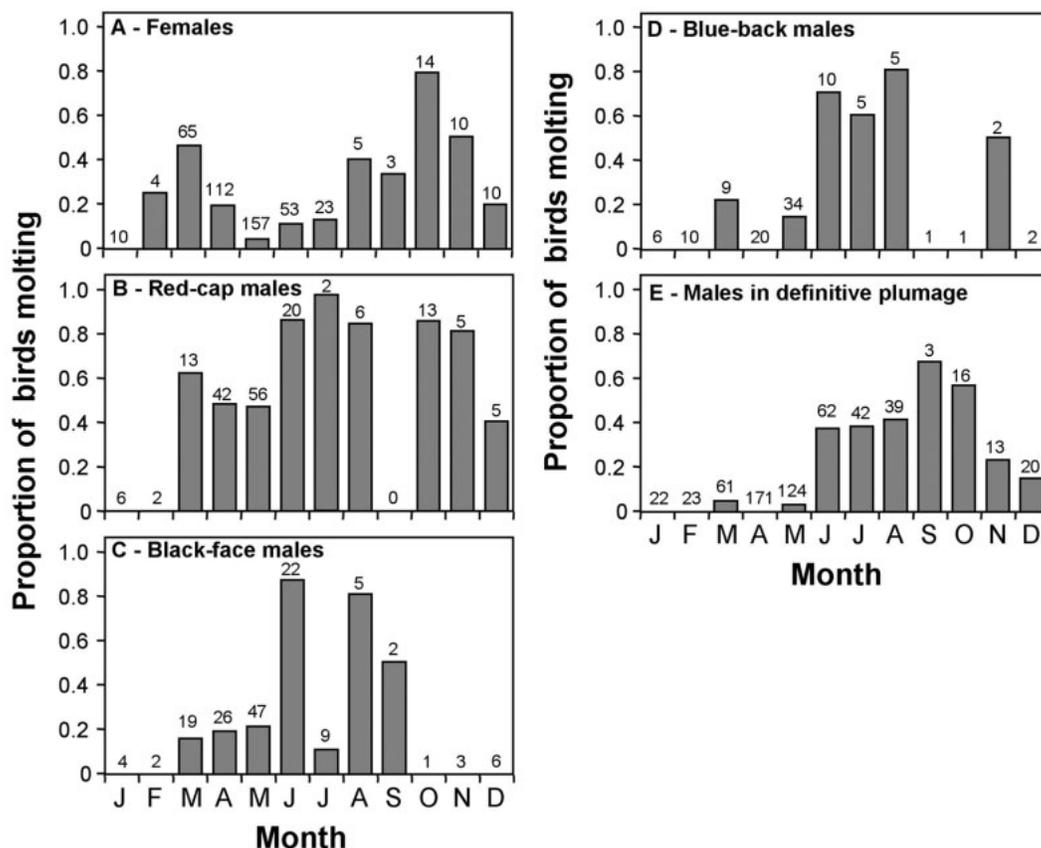


FIG. 3. Monthly proportions of Long-tailed Manakins showing signs of molt at time of capture for birds in different plumage stages. Data are from mist-net captures in northwestern Costa Rica ($n = 867$) and museum specimens ($n = 585$). Data are pooled across years, and numbers above bars indicate total number of birds captured in each month. (Although plumage stages are indicated on each graph, letters are included to facilitate referencing in the text and comparisons with Figure 1.)

males exhibited a peak of molt activity between June and August, which corresponded to their complete third and fourth prebasic molts, respectively.

Males in definitive plumage exhibited the simplest yearly molt activity pattern (Fig. 3E). Very few (<5%) males showed any signs of molt from March to May. By June, more than one-third of definitive-plumaged males examined were molting, and molt activity in these males peaked in September.

DISCUSSION

By examining the plumage characteristics of 1,315 color-banded individuals in northwestern Costa Rica and 585 museum specimens, we

documented age- and sex-related variation in plumage maturation and molt timing in Long-tailed Manakins. Male plumage development progressed in discrete, age-specific categories from an all-green juvenal plumage, through three distinct predefinitive plumages, to a definitive adult plumage in fifth-year and older birds. This represents the longest delay yet reported in any manakin (see Foster 1987, Duval 2005). Although variation in female plumage was more subtle, some females acquired male-like plumage features as they aged. Our findings have important implications for elucidating the adaptive significance of delayed plumage maturation, and the potential signal function of intraspecific variation in plumage, in Long-tailed Manakins and other species.

Male plumages.—Male Long-tailed Manakins progressed through the following plumage sequence. Hatch-year (juvenile) males were olive green throughout; second-year (red-cap) males were olive green with some red on the crown; third-year (black-face) males were olive green with a red crown and a black facial mask or hood; fourth-year (blue-back) males were a mixture of green and black with a red crown and a blue and green mantle; and fifth-year and older (definitive) males were black with a red crown patch and a blue mantle. This plumage sequence can be summarized by the following heuristic: from (1) a green-plumaged bird, (2) add red, (3) add black, (4) add blue, (5) take away green. Our conclusions are consistent with those of McDonald (1989a, 1993a) but differ from those of Foster (1987). In Foster's (1987) sequence, red-cap and black-face males were included in the same age class, whereas blue-back males were separated into two age classes. Differences in interpretation of the red-cap stage may reflect the fact that birds in red-cap plumage occasionally have some black feathers on the face, particularly once they begin to molt in the early breeding season. Foster (1987) therefore (incorrectly) included black-face birds in the red-cap plumage stage. The discovery that second-year birds can be aged on the basis of differences in wing feathers now makes this distinction infallible (see also Ryder and Durães 2005). Foster's (1987) differentiation of males with blue, black, and green plumage into two stages likely reflects a misinterpretation of the extreme variation in the proportions of these colors in the third basic plumage. Nevertheless, our data from numerous plumage transitions show that the presence of blue mantle feathers and black body feathers (other than those on the head) is a robust criterion for defining the third basic (blue-back) plumage.

Although there was considerable variation within plumage stages of male Long-tailed Manakins, there was little overlap between plumage stages. Two apparent exceptions to the sequence involved males that were first captured in green plumage and recaptured the following year in black-face plumage. These birds were captured before it was discovered that green birds could be aged on the basis of retained juvenile wing feathers, however, and it is likely that these were second-year males without a red crown patch, as opposed to juvenile-plumaged

hatch-year males. Indeed, in a separate analysis, Clay (2001) identified two museum specimens as second-year males with all-green crowns. Moreover, the males in our study were captured in March and April, and would have fledged from exceptionally early nests if they were, in fact, hatch-year males. Two other males apparently molted from a red-cap plumage into a blue-back plumage. If, in fact, these four males represent anomalous sequence transitions, they correspond to accelerations of the typical sequence. However, because of the rarity of these anomalies ($\leq 1.8\%$ of predefinitive plumage transitions), they probably occur arbitrarily rather than as a response to selective pressure on males to accelerate through the maturation process. Taken together, our findings strongly suggest that plumage coloration is a highly consistent signal of age in young males until they reach their fifth calendar year. This conclusion has two important implications. First, our data confirm that young males can be aged reliably in the field on the basis of plumage features. Second, our data support the hypothesis that plumage variation can serve as a social signal of age in young males (McDonald 1993a).

Social signaling in males.—The complex social system of Long-tailed Manakins is dependent on the development of long-term cooperative alliances between males (Foster 1977; McDonald 1989a, b, 1993a). Males must spend several years working their way up the dominance hierarchy to eventually have the opportunity to display for females and, in a minority of males, to copulate. The social stability of these mating queues appears to be strictly enforced by female mate choice, given that females will often leave the dance perch at the first sign of disruption by males other than the dominant males (Foster 1987; McDonald 1989a, 1993a). The evolution of predefinitive male plumages is beneficial to both subordinate and dominant males in this type of social system. For dominant males, the predefinitive plumage of young males immediately identifies them as not posing a threat to their reproductive success (McDonald 1989b, McDonald and Potts 1994), which likely reduces the amount of aggression that young males will receive from older males. Indeed, in the congeneric Blue Manakin (*C. caudata*), the amount and intensity of aggression shown by dominant males toward subordinate individuals decrease with decreasing age of the target

individual (Foster 1987). In addition, the evolution of age-specific plumages can provide additional information about the status of males within the dominance hierarchy. In support of this hypothesis, a taxidermy mount experiment revealed that male Long-tailed Manakins responded more strongly to males in definitive plumage than to males in predefinitive plumage (McDonald 1993a). Moreover, responses were often initiated by non-alpha males, which suggests that the model intruders posed a threat to established male–male alliances rather than a risk of stolen copulations (McDonald 1993a). These observations are paralleled in Blue Manakins, in which aggression directed toward a transgressor was often initiated by males of intermediate rank and directed toward the individuals nearest them in the hierarchy (Foster 1981). These studies suggest that males are most likely to challenge males of similar rank in a hierarchy and, presumably, against whom they have the greatest probability of success. The obverse of this is that males are also most likely to have to defend their own positions against challenges from members of their own or adjoining age cohorts. A model presentation experiment in another species with a graded, multiyear delay in plumage maturation, the Hawaiian 'Elepaio (*Chasiempis sandwichensis*), yielded similar findings (VanderWerf and Freed 2003).

Female plumage.—Extreme sexual dichromatism is characteristic of the family Pipridae. Male manakins are usually brightly colored, whereas females are typically olive green (Prum 1997, Doucet et al. 2006). Here, we documented considerable variation in the plumage of female Long-tailed Manakins. Some females developed variable amounts of red or tawny coloration in the crown, reminiscent of the red crowns of males, and a small proportion of females developed black feathers on the face, head, wing, or tail. Older females were more likely than young females to develop red or tawny crowns, and, on average, more than five years elapsed between initial female captures and the appearance of red in their crowns. Female ornamentation may have evolved as a byproduct of genetic correlations between male and female traits (Lande 1987, Amundsen 2000). Strong selection for elaborate ornaments in males, combined with weaker selection against these traits in females, could lead to the expression of ornamental coloration in females, even if

it is maladaptive. Because females are solely responsible for parental care in manakins, they should experience strong natural selection for crypsis (Martin and Badyaev 1996), particularly given that rates of nest predation are quite high in the tropics (Stutchbury and Morton 2001). Yet bright female coloration has been reported in a number of manakin genera (Graves 1981) and, in Long-tailed Manakins, females with red crowns were more likely to express other male-like plumage characteristics. Our documented association between ornamental color and age in older females could be proximately mediated by age-related hormonal changes (Kimball and Ligon 1999). In some cases, male-like plumage characteristics other than crown color disappeared after the following molt, which suggests that they may have resulted from adventitious feather loss and replacement at a time of year when environmental cues, such as photoperiod or daytime light intensity (Gwinner 2003), led to the growth of more male-like plumage.

A less likely possibility is that the development of red crown coloration in older females serves a social signaling function. Because of its association with age, red crown coloration could signal a female's longevity or viability. Such a signal may be useful to males, who could optimize their display intensity or sperm allocation by investing more in females they deem to be of high quality (e.g., Amundsen 2000, Werner and Lotem 2003), a pattern that may explain some of the variation in male display intensity in this species. Alternatively, a signal of female age may be useful to young females, whose mate choice decisions could be influenced by those of older, experienced females when multiple females observe displaying males together (Dugatkin and Godin 1993, Doucet et al. 2004). Comparative analyses of the relationship between male and female ornamentation, in combination with intraspecific empirical investigations of the proximate control and signal function of female traits, will help to identify the relative merit of these hypotheses in explaining the evolution of bright female plumage in manakins.

Timing of molt.—Long-tailed Manakins undergo a post-juvinal molt within four months of hatching and subsequently undergo a prebasic molt each year. The first prebasic molt is incomplete: birds of both sexes retain their juvinal remiges and distal greater coverts. Second-year birds

also retain the yellow-orange mouth color typical of nestlings of this species (Foster 1976). A similar pattern of delayed maturation in mouth color has been reported in one species of bowerbird (Frith and Frith 2004). Given the considerable number of species that show delayed maturation in iris and soft-part color (Lawton and Lawton 1986), delayed maturation in mouth color may be relatively widespread and should be investigated in other species.

We found significant age- and sex-based variation in timing of molt. Females exhibited an early peak of molt activity in February and March. Second-year females were more likely to show signs of early molt than older females. Nevertheless, fewer than half of females showed signs of early molt activity, and this molt was limited to some body and head feathers. Molt activity was low from May through July in females and increased in August to a second peak, corresponding to the complete prebasic molt, in October. The decrease in molt activity from April to July may reflect evolutionary pressure to avoid the costs of molt-breeding overlap (Foster 1974), because this period corresponds to the peak of female nesting activity (Foster 1976). Molt and breeding are both energetically demanding (e.g., Murphy and King 1992, Lindstrom et al. 1993). As such, physiological and ecological trade-offs are expected to occur between these two life-history traits (Foster 1975a). Theory therefore predicts that molt and breeding should be temporally segregated, yet molt-breeding overlap has been reported in numerous tropical and temperate passerines (Foster 1975b, Pyle 1997) and, as we have shown here, occurs at the population level in Long-tailed Manakins (Fig. 3). However, our data show that in May, June, and July, <15% of females exhibited any signs of molt. Later in the season, females' primary resource-consuming activity can switch from breeding to molt (see Foster 1975b), which may explain the second, most prominent peak of female molt activity in October.

Though they provide no parental care, male Long-tailed Manakins may expend considerable amounts of energy in breeding-related activities and are, therefore, also expected to avoid molt-breeding overlap. Dominant (alpha and beta) males perform energetically demanding dance displays for females and sing duets at high rates to attract females to their leks ($\leq 5,000$ vocalizations per day; Foster 1977,

McDonald 1989b, Trainer and McDonald 1993). By June, there is usually a notable decrease in male display activity, especially at the least successful leks (S. M. Doucet and D. B. McDonald unpubl. data), which, as we have shown here, corresponds to a sharp increase in proportion of males in definitive plumage showing signs of molt. Females, on the other hand, are known to nest until at least July, and probably until September (Foster 1976). Male display activity is intrinsically linked to the availability of receptive females. A successful copulation, however, marks only the beginning of a female's parental responsibilities. Thus, the reproductive periods of dominant males and females are inherently staggered, which may explain why the post-breeding molt of males in definitive plumage peaks earlier than that of females. Moreover, many definitive-plumaged males occupy subordinate ranks at leks. These males are expected to expend much less energy on display than dominant males and to curtail their breeding season activities sooner.

Over the course of the breeding season, young male Long-tailed Manakins in predefinitive plumage form affiliations with other males at particular lek sites, often practicing courtship displays on dance perches used by dominant males. Young males are tolerated at dance perches only in the absence of females, however, because only dominant males display for, and copulate with, females (McDonald 1989a). Moreover, young males are resighted at leks less frequently than older males (McDonald 1989a), which suggests that they invest less time and energy in breeding-season activities than older males. Thus, young males can begin molting earlier in the season than older individuals. Correspondingly, blue-back and black-face males exhibited an earlier peak of molt activity than males in definitive plumage.

Early molt in red-cap males is more difficult to interpret. Many males in red-cap plumage began to molt in March, at the onset of the breeding season. Moreover, this molt was apparently restricted to the crown and head. Indeed, these males often molted in additional red crown feathers and black-face feathers, thereby accelerating their transition into black-face plumage. Dominance interactions among males of the same age cohort may explain this early molt. If crown and mask color allow males to assert their dominance over members of their

own age cohort, then selection might favor the acceleration of such a molt. Males in predefinitive plumages, particularly younger ones, are subject to opposing selective forces: by signaling their lesser age, the plumages may reduce the aggression directed toward them by older males; at the same time, however, it might benefit them to develop, as much as possible, the traits that signal their prowess to males of the same cohort (Foster 1987, McDonald 1993a). This conflict may explain why some species progress through several distinct predefinitive plumage stages rather than molting into the same predefinitive plumage for several years, as has been documented in numerous other species (e.g., Frith and Beehler 1998, Frith and Frith 2004).

Implications.—Male Long-tailed Manakins in predefinitive plumage have testes capable of producing sperm (Foster 1987). Thus, delayed plumage maturation in this species represents an instance of heterochrony and, more specifically, of neoteny (i.e., a slowing down of somatic maturation in relation to sexual maturation; Lawton and Lawton 1986). Mean testis size among 60 definitive-plumaged males was $29.3 \pm 16.16 \text{ mm}^3$ (Foster 1987). Interestingly, the testis size of a beta male known to have been in definitive plumage for several years was 75 mm^3 , nearly three standard deviations above the mean (D. B. McDonald unpubl. data), which suggests that plumage maturation likely precedes full testis maturation in this species. Long-tailed Manakins may therefore exhibit both neoteny and progenesis (where somatic maturation precedes reproductive maturation). Lawton and Lawton (1986) proposed that heterochronic trends in plumage, iris, and soft-part maturation are associated with complex social organization within the Corvidae and may have played a role in speciation among closely related corvids. As empirical investigations of delayed plumage maturation become more widely available, particularly among tropical species, it will be possible to examine patterns of heterochrony, and the complex mixing of neotenic and progenetic features, in other groups that vary in degree of social organization, including other manakins (Prum 1997). The increasing availability of well-supported phylogenies will greatly facilitate these comparative investigations. Studies of delayed plumage maturation across a wider variety of

taxa, particularly species that differ from the typical north-temperate pattern, are likely to reveal that the adaptive significance of delayed plumage maturation cannot be encompassed by a single hypothesis. Moreover, accumulating evidence of interspecific variation in both patterns and consequences of delayed plumage maturation suggest broader evolutionary implications than we originally anticipated.

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