Acquisition of definitive adult plumage in male Blue Manakins Chiroxiphia caudata

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O tangará *Chiroxiphia caudata* é uma das mais belas aves neotropicais, com os machos adultos exibindo uma vistosa plumagem azul, preta e vermelha. A primeira plumagem dos machos, contudo, assemelha-se àquela das fêmeas, sendo completamente verde. A partir da muda pré-formativa, a colorida plumagem dos machos adultos é lentamente adquirida, passando por diversos estágios intermediários. Aqui são descritos nove estágios desde a plumagem juvenil totalmente verde até a plumagem definitiva. A lenta aquisição da plumagem masculina adulta é considerada vantajosa, pois a maior tolerância dos machos adultos com aqueles exibindo plumagens intermediárias, durante as exibições pré-nupciais coletivas, pode facilitar o processo de aprendizado do elaborado ritual de côrte pelos imaturos.

Manakins (Pipridae) are among the most beautiful of Neotropical birds. They are small understorey and subcanopy passerines of forest habitats in Middle and South America¹¹. Although some adult female manakins display male-like plumage characters^{3,4,10,12}, most females and young males possess olive-green plumage, while adult males of most species are brightly coloured with yellow, red, blue, white and black. These plumages are essential for polygamous birds such as manakins with elaborate courtship displays. Males of many species display in groups at special leks where they compete for females. Following copulation, females alone nest build, incubate the eggs and care for the young^{10,11}.

Young male manakins possess female-like juvenile plumage replaced by multiple intermediate plumages after a few months. Definitive adult plumage is only acquired at 2–5 years old^{3,5,7,9–11}. Delayed acquisition of adult plumage in male *Chiroxiphia* spp. has been related to the complex dominance hierarchy at leks^{3,6,11}.

Because some field studies related to manakins may be obscured by the delayed plumage maturation in males, the acquisition of adult plumage has been studied in detail^{3,4,6–8}. Here we describe plumage succession with age in male Blue Manakins *Chiroxiphia caudata*, based on banded birds in south-east Brazil.

Material and Methods

To recognise the different stages of the male plumage sequence in Blue Manakins, we included records of males with intermediate plumages observed or mist-netted during field work since 1990 at various localities in the state of Rio de Janeiro, south-east Brazil. Ten banded birds retrapped several times during the acquisition of definitive male plumage enabled us to recognise the different stages of plumage succession (Table 1). These birds were trapped and banded during a

capture / recapture programme of forest birds conducted between July 1995 and June 1997 near Guapimirim (22°32'S 42°59'W). Each manakin was marked using a numbered aluminum leg band and its plumage categorised by colour. Plumage and moult terminology is modified from the sequence described for other *Chiroxiphia* spp. 3.6.7 and other tropical birds 13.

Results and Discussion

We can recognise nine stages in the plumage succession of male Blue Manakins (Fig. 1). Although plumage stages have already been proposed for this species¹², our classification provides a more objective description of this succession. The stages are as follows:

- Stage 1 (juvenile plumage). Female-like juvenile plumage entirely dull olive-green.
- Stage 2 (formative plumage). Plumage dull olive-green with orangish forehead. Some females have orange forehead mottled green like young males at this stage^{1,5,12}.
- Stage 3 (formative plumage). Similar to Stage 2, but entire crown orange-red from forehead to nape. Sometimes referred to as 'redcap' plumage.
- Stage 4 (formative plumage). Plumage dull olive-green with crown orange-red and blackish mask. Sometimes referred to as 'black-face' plumage.
- Stage 5 (pre-definitive plumage). Black head with crown orange-red. Breast, belly and undertail-coverts greyish blue. Mantle, rump and wings dull olive-green. Tail bluish green.
- Stage 6 (pre-definitive plumage). Black head with orange-red crown. Breast, belly, undertail-coverts and rump cerulean blue. Mantle and wings dull olive-green. Tail bluish green.

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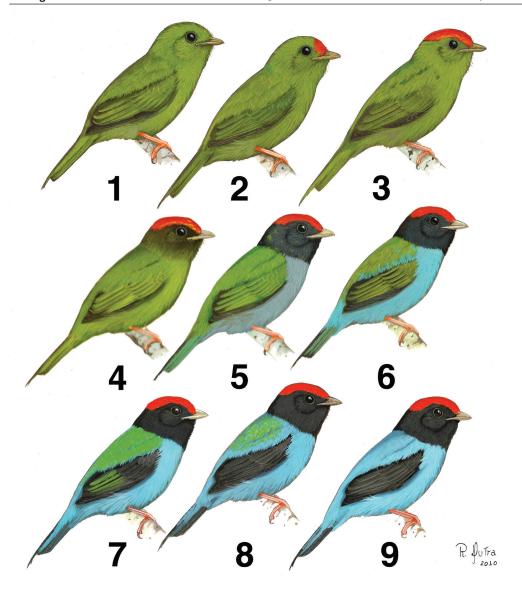


Figure I. Stages of plumage succession in male Blue Manakins Chiroxiphia caudata (Raphael Dutra)

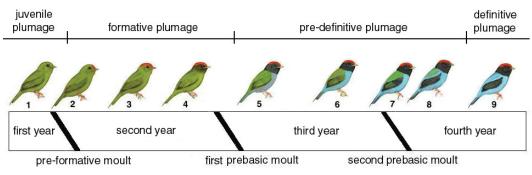


Figure 2. Timeline of plumages and moults in male Blue Manakins Chiroxiphia caudata (Rafael Dutra)

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Table I. Plumage stages of ten male Blue Manakins Chiroxiphia caudata recaptured several times during the acquisition of definitive plumage.

Individual I	First capture Stage I (8 Dec 1995)	First recapture Stage 3 (6 Jul 1996)	Second recapture	Third recapture
2	Stage 4 (7 Jan 1996)	Stage 6 (7 Dec 1996)	Stage 7 (28 Mar 1997)	Stage 8 (21 Jun 1997)
3	Stage 2 (24 Mar 1996)	Stage 6 (21 Jun 1997)		
4	Stage 6 (27 Apr 1996)	Stage 7 (25 Jan 1997)		
5	Stage 3 (6 Jul 1996)	Stage 5 (25 Jan 1997)	Stage 5 (29 Mar 1997)	
6	Stage 3 (6 Jul 1996)	Stage 4 (28 Sep 1996)	Stage 6 (12 Apr 1997)	
7	Stage 3 (7 Jul 1996)	Stage 4 (7 Dec 1996)		
8	Stage 6 (22 Sep 1996)	Stage 8 (12 Apr 1997)		
9	Stage I (9 Nov 1996)	Stage 2 (16 Feb 1997)		
10	Stage 8 (28 Mar 1997)	Stage 9 (2 May 1997)		

- Stage 7 (pre-definitive plumage). Like Stage 6, but mantle bluish green, wings black with secondaries greenish and tail black with elongated central rectrices cerulean blue.
- Stage 8 (pre-definitive plumage). Similar to Stage 7, but wings all black and mantle greenish blue.
- Stage 9 (definitive plumage). Definitive adult male plumage. Black head with crown orange-red. Breast, belly, undertail-coverts, mantle and rump cerulean blue. Black wings and tail, but elongated central rectrices cerulean blue.

Young males are all green in juvenile plumage (Stage 1) but soon acquire an orange crown (Stages 2-4). The first orange feathers emerge at three months old during a partial pre-formative (or post-juvenile) moult (Stage 2)^{2,6,12}. In the second year this plumage is retained, but the orange-red crown becomes complete (Stage 3) and blackish feathers emerge to form a dark mask (Stage 4). In the third year of life a pre-definitive plumage (Stage 5–7) appears as a result of the first prebasic moult. Bluish feathers appear initially on the ventral region (Stage 5) and subsequently on the rump and central rectrices (Stage 6). During the second prebasic moult in the third year, greenish feathers are replaced by black feathers in the tail (except the bluish central pair) and wings (initially the coverts, the primaries [Stage 7] and finally the secondaries), although some greenish feathers remain in the scapulars (Stage 8) post moult. Definitive plumage is acquired once the green scapulars are totally replaced by blue feathers (Stage 9) in the fourth year (Fig. 2).

The development of adult male plumage occurs similarly in all *Chiroxiphia*^{6,7}. However,

Long-tailed Manakins *C. linearis*, from Middle America, attain definitive adult plumage later than Lance-tailed Manakins *C. lanceolata* of northern South America, and *C. caudata*⁴. Species-specific differences in the delayed acquisition of definitive plumage may be related to the time required to attain a breeding position in the hierarchy of each species⁶.

Delayed acquisition of definitive adult male plumage in Blue Manakin has been viewed as a response to the tendency to tolerate females expressed by older males. Adult males are less aggressive towards intermediate-plumaged males than to other adult males, meaning that young males increase their probability of mating, or at least become more experienced to display in groups⁶. Adult male Long-tailed Manakins are also more aggressive toward other adult males than to males in pre-definitive plumage⁷. Decreased vulnerability to predation may also explain the retention of juvenile plumage characters for longer periods.

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