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**PROGRAMA DE PÓS-GRADUAÇÃO EM DIVERSIDADE BIOLÓGICA E**  
**CONSERVAÇÃO**

**Dissertação de Mestrado**

**COMPORTAMENTO REPRODUTIVO DO TANGARÁ-DANÇARINO,  
*CHIROXIPHIA CAUDATA* (AVES, PIPRIDAE) EM UMA ÁREA DE MATA  
ATLÂNTICA.**

**Paulo Victor Queijo Zima**

**Orientador: Mercival Roberto Francisco**

**SOROCABA - 2015**



Macho adulto de *Chiroxiphia caudata*



Fêmea de *Chiroxiphia caudata*

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DANÇARINO, *Chiroxiphia caudata* (AVES, PIPRIDAE) EM  
UMA ÁREA DE MATA ATLÂNTICA

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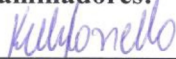
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Ao quarto dia do mês de fevereiro de 2015, às 14 horas, na sala AT.12, localizada no prédio da Biblioteca, da Universidade Federal de São Carlos, *Campus* Sorocaba, reuniu-se a Banca Examinadora composta pela Profa. Dra Kelly Cristina Tonello, da Universidade Federal de São Carlos – *Campus* Sorocaba, Dr. Marco Aurélio Pizo Ferreira, da Universidade Estadual Paulista “Júlio de Mesquita Filho” – UNESP Rio Claro, presidida pelo Prof. Dr. Mercival Roberto Francisco para a defesa de dissertação de mestrado do aluno **PAULO VICTOR QUEIJO ZIMA**, intitulado “Comportamento reprodutivo do Tangará-Dançarino, *Chiroxiphia caudata* (Aves, Pipridae) em uma área de Mata Atlântica”. As atividades seguiram de acordo com o regulamento do Programa, tendo o candidato recebido o conceito final: Aprovado (aprovado/reprovado). Nada mais a declarar, eu Luciana Missae Kawamura lavro esta ata que foi assinada pelos membros da Banca Examinadora.

  
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“Talvez não tenha conseguido fazer o melhor,  
mas lutei para que o melhor fosse feito.  
Não sou o que deveria ser, mas Graças a Deus,  
não sou o que era antes.”  
(Marthin Luther King)

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## INTRODUÇÃO GERAL

As respostas evolutivas, comportamentais e ecológicas das populações às condições ambientais onde vivem são contemplados pelos estudos de história de vida (Ricklefs 2000). A evolução dos parâmetros reprodutivos é um importante quesito dos estudos de história de vida em Aves (Böhning-Gaese et al. 2000, Martin 1995, Cooper et al. 2005). Há vários trabalhos que vêm discutindo que ninhadas maiores, menos ninhadas por ano e períodos de cuidado parental menores, são padrões de espécies de aves de regiões temperadas do hemisfério norte, quando comparadas a aves tropicais e do hemisfério sul (Lack 1947, Skutch 1949, Lack & Moreau 1965, Ricklefs 1969). Grande parte dos estudos têm dado mais importância ao tamanho das ninhadas, levando pouco em consideração o número de ninhadas por temporada reprodutiva e períodos de cuidado parental (Cooper et al. 2005).

### *A família Pipridae*

Os componentes da família Pipridae são aves de pequeno porte (geralmente na faixa de peso de 8 a 30 gramas), corpo robusto, cauda curta e bico curto e ainda que largo quando de boca aberta (Ridgely & Tudor, 1994, Sick 2001). São reconhecidos por possuírem um alto grau de dimorfismo sexual, dado que os machos de maneira geral, possuem grande parte da cobertura na cor preta, contrastando com cores mais chamativas como azul, vermelho, laranja, amarelo, entre outras. Além disso, podem possuir penas modificadas nas asas e na cauda geralmente utilizadas nas exibições de corte. Já as fêmeas e os jovens possuem coloração verde oliva, sendo geralmente muito parecidas entre as espécies (Sick 2001). São aves consideradas quase exclusivamente de floresta tropical. Passam quase todo o tempo nos estratos médios e inferiores da floresta, raramente atingindo os estratos mais altos das copas e vivem principalmente em

ambientes com altitudes abaixo de 1000 m (Ridgely & Tudor, 1994). A principal fonte de alimentos do grupo é composta por pequenos frutos, podendo ser complementado com insetos (Snow 1985).

O grupo é famoso por suas exibições de corte peculiares. Fazem parte do seu repertório muitos movimentos complexos e elaborados, mostrando como principal característica grupos de machos (“leks”) com organização social muito complexa que, de um ano para outro, continuam a exibir-se nos mesmos locais (arenas de exibição) (Foster 1981). No entanto, um fato curioso é que este comportamento realiza-se mesmo na ausência de fêmeas. Os cruzamentos são realizados sempre por uma minoria de machos dominantes, e no caso do gênero *Chiroxiphia*, as exibições são cooperativas e o macho dominante do lek realiza todas as cópulas (McDonald 1989).

Em todos os piprideos com comportamento reprodutivo estudados, apenas as fêmeas foram encontradas como responsáveis pelas tarefas relacionadas a nidificação, não havendo formação de casais para a época reprodutiva (Snow 2004). No entanto, informações básicas quanto a biologia reprodutiva são pouco conhecidas. Apenas 29 das 51 espécies que compõem a família (Remsen et al. 2014) possuem ninhos descritos. *Ceratopipra erythrocephala* (Tostain 1988), *Lepidotrrix coronata* (Skutch 1969), *Manacus aurantiacus* (Skutch 1969), *Manacus manacus* (Oniki & Willis 1983, Snow 1962), e *Chiroxiphia lanceolata* (DuVal 2007), são as únicas espécies com períodos de incubação descritos de maneira precisa, e períodos de ninhegos são conhecidos somente para *Ceratopipra rubrocapilla* (Pinto 1953), *L. coronata* (Skutch 1969), *C. lanceolata* (DuVal 2007), *M. aurantiacus* (Skutch 1969), *Manacus vitellinus* (Worthington 1982), and *M. manacus* (Oniki & Willis 1983; Snow 1962). Além disso, surpreendentemente, não existem publicações sobre cuidado parental detalhadas.

### O Gênero *Chiroxiphia*

A organização social e os repertórios de exibição dos componentes de *Chiroxiphia* estão, provavelmente, entre os mais elaborados dentre as todas aves (Snow 2004). No gênero, a cooperação entre machos no display sexual apresenta-se obrigatória para que haja acasalamento, em todas as espécies do gênero (*C. pareola*, Snow, 1963; *C. linearis*, Foster, 1977; *C. caudata*, Foster, 1981). Nos *Chiroxiphia*, a corte consiste na emissão de sons e na dança cooperativa de exibição, sendo esta “convocada” pelo macho alfa (Sick 2001). Com a presença de uma fêmea o grupo (ou par/trio) de machos começa uma elaborada dança em um poleiro de exibição (Slud 1957, Snow 1963). Em caso de receptividade da fêmea, apenas um dos machos, o alfa, permanece para completar a corte e acasalar (Foster 1981, McDonald 1989). De acordo com o trabalho feito por McDonald (1989) das 263 cópulas acompanhadas por ele, apenas quatro não foram realizadas por machos alfa. Foi visto por DuVal (2007) que as áreas e poleiros de exibição são mantidos e reutilizados por vários anos. As espécies do gênero possuem provavelmente um tempo de vida de 12 anos ou mais (Wiley 1991). A corte cooperativa é incomum entre os vertebrados, e por isso, estudos com o gênero *Chiroxiphia* são importantes para se conhecer como evoluiu esse tipo de comportamento social (DuVal 2005, Krakauer 2005).

Ninhos e ovos foram descritos para as 5 espécies pertencentes ao gênero (Hallinan 1924, Pinto 1953, Foster 1976, Hazlehurst & Londoño 2012), no entanto outros dados referentes a reprodução como períodos de incubação e de ninhegos foram descritos na natureza apenas para *C. lanceolata* (DuVal 2007) e em cativeiro para *Chiroxiphia pareola* (Pinto 1953).

*O Tangará-dançarino, Chiroxiphia caudata*

O Tangará-dançarino, *C. caudata*, é um piprídeo que tem como características físicas as pernas avermelhadas, os machos são de um azul destacado com boné vermelho; cabeça, asa e penas externas da cauda pretas; as penas centrais da cauda são mais alongadas. As fêmeas são de cor oliva, sendo mais claras na região inferior do corpo; as penas centrais da cauda são levemente mais longas (Ridgely & Tudor 1994, Willis & Oniki 1988). São bem comuns em florestas úmidas, florestas secundárias e nas bordas da região sudeste do Brasil, nordeste da Argentina e Leste do Paraguai (Ridgely & Tudor 1994). No Brasil sua distribuição se dá em um ecossistema muito ameaçado, a Mata Atlântica.

O sistema de acasalamento de *C. Caudata* é um tipo de poligamia, onde os machos agregam-se em locais tradicionais, os leks, com o intuito de realizar exposições pré-nupciais cooperativas. Estes leks são compostos geralmente de grupos de 2 a 8 machos (Foster 1981, Francisco et al. 2009). Na cerimônia nupcial, os machos dançam de maneira muito agitada e coordenada, mostrando-se a uma fêmea, o último indivíduo alça voo mais alto e fica no ar por mais tempo sobre a fêmea, batendo as asas mais rapidamente e ao fim, emite um som diferenciado muito agudo marcando o fim da apresentação. O ritual tem duração média de 30 segundos podendo prolongar-se por até dois minutos. Ao que parece o macho que finaliza a cerimônia é o indivíduo dominante do lek (Sick 2001).

Um fato muito interessante que ocorre nesta espécie é o de machos imaturos se colocarem no papel de fêmeas quando estas não estão presentes na dança, porém essa dança costuma ser menos coordenada (Sick 2001).

As únicas informações acerca da atividade reprodutiva da espécie são descrições de ninho, que é uma taça rasa, pendurado em uma forquilha horizontal com materiais

soltos a que pendem da parte inferior da taça (Euler 1900, von Ihering 1902, Foster 1977), e descrições de ovos feitas por Foster (1977) e Fraga e Narosky (1985), sendo esses de fundo bege com manchas marrom escuras com maior concentração no pólo maior do ovo.

Para que metas de manejo sejam confeccionadas mostra-se necessário, para qualquer espécie, obtermos informações sobre ecologia e comportamento de maneira detalhada (Collar et al. 1992, Willis & Oniki 1992, Ridgely & Tudor 1994, Sick 2001, Willis 2003). Porém não há muitas informações sobre a biologia reprodutiva na natureza para as espécies do gênero *Chiroxiphia*.

## **OBJETIVOS**

Neste estudo nós pretendemos trazer a primeira descrição detalhada do comportamento reprodutivo do Tangará dançarino, *Chiroxiphia caudata*, e uma revisão detalhada sobre os ninhos da família Pipridae. Nossos objetivos específicos são:

- 1) Apresentar informações de fenologia reprodutiva, habitat de nidificação, períodos de incubação e ninhegos, sucesso reprodutivo e cuidado parental de uma população de um contínuo preservado de Mata Atlântica no Estado de São Paulo;
- 2) Discutir a arquitetura dos ninhos da família Pipridae em um contexto filogenético e;
- 3) Comparar as características de história de vida ligadas a reprodução entre as regiões tropical e equatorial

## CAPÍTULO 1

Breeding Behavior of the Atlantic Forest-endemic Blue-Manakin, *Chiroxiphia caudata*

(Aves, Pipridae)

Resultados na forma de um artigo a ser submetido para o periódico The Wilson  
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RRH: MAJOR ARTICLES

Breeding Behavior of the Atlantic Forest-endemic Blue-Manakin, *Chiroxiphia caudata*  
(Aves, Pipridae)

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ABSTRACT.---The family Pipridae is endemic to the Neotropics, having frugivorous habits. Males of some species make complex sexual displays to attract the females, and they live in the middle stratum of tropical forests. Of 51 species, 29 have their nests described, five have incubation periods descriptions, and six have nestling periods reported. The Blue Manakin, *Chiroxiphia caudata*, is common in humid and secondary forests of southeastern Brazil, northeastern Argentina and eastern Paraguay and its breeding biology is poorly documented. Here analyzed 36 active nests in two breeding seasons (2013/2014 and 2014/2015) in a well-preserved Brazilian Atlantic Forest continuum. Nests were swallow cups hung by their rims in horizontal forks, built in bushes or saplings, over or near forest streams. Reproductive activities were recorded from October to February and clutch sizes were invariably two eggs. Incubation period was 18 days, and nestling period was 15 - 16 days. Estimated overall nesting success, from egg-laying to fledging, was 40%, being higher than most studies on piprids that have been conducted in disturbed habitats. Our data give support to the theory that in the Pipridae family only females provide parental care.

Key Words---Nesting biology, parental care, nesting success, breeding life-history traits.



The Pipridae are small frugivorous birds endemic to the Neotropics, distributed mainly in the understory of humid forests. This is a remarkable group of birds, especially because of male conspicuous colors and complex sexual displays (Ridgely and Tudor 1994, Sick 2001, Snow 2004). While pre-nuptial behavior has attracted attention of many researchers (Foster 1977; Foster 1981; McDonald 1989; Wiley 1991; Krakauer 2005; Loiselle et al. 2006; DuVal 2007; Francisco et al. 2009), aspects of their nesting biology are poorly documented. Of the 51 species (Remsen et al. 2014), 29 had their nests described. Precise incubation periods are reported for Golden-headed Manakin, *Ceratopipra erythrocephala* (Tostain 1988), Blue-crowned Manakin, *Lepidotrrix coronata* (Skutch 1969), Orange-collared Manakin, *Manacus aurantiacus* (Skutch 1969), and White-bearded Manakin, *M. manacus* (Oniki and Willis 1983; Snow 1962), and nestling periods are known for Red-headed Manakin, *C. rubrocapilla* (Pinto 1953), *L. coronata* (Skutch 1969), Lance-Tailed Manakin, *Chiroxiphia lanceolata* (DuVal 2007), *M. aurantiacus* (Skutch 1969), Golden-collared Manakin, *M. vitellinus* (Worthington 1982), and *M. manacus* (Oniki and Willis 1983; Snow 1962).

The genus *Chiroxiphia* is composed by five species that are characterized by cooperative courtship displays, in which a number of males aggregate into traditional leks coordinated by an alpha male that have access to most copulations (Foster 1977; Foster 1981; McDonald 1989; DuVal 2007; Francisco et al. 2009). Although nests and eggs have been described for all of the species (Hallinan 1924, Pinto 1953, Foster 1976, Hazlehurst and Londoño 2012), further information is scarce. The Blue Manakin, *Chiroxiphia caudata*, is common in humid and secondary forests of southeastern Brazil, northeastern Argentina and eastern Paraguay (Ridgely and Tudor 1994), and nesting information for this species is limited to nests and eggs descriptions presented by Euler (1900), Von Ihering (1902), Foster (1977, 1981), and Fraga and Narosky (1985).

Here we present the first detailed description of the reproductive behavior of the Blue Manakin and we provide a review on Pipridae nesting biology. Our specific objectives were to: 1) present information on breeding phenology, nesting habitat, incubation and nestling periods, nesting success, and parental care for a population from a continuous and undisturbed Atlantic Forest area from State of São Paulo, southeastern Brazil, 2) discuss the nest architecture of the Pipridae in a phylogenetic context, and 3) compare breeding life history traits of Pipridae from tropical and equatorial regions.

## METHODS

*Study Area* - The present study was performed in Carlos Botelho State Park (PECB) (24° 06' 55''–24° 14' 41'' S, 47° 47' 18''–48° 07' 17'' W), São Paulo State, Brazil. This park contains 37,644 ha mainly of primary Atlantic Forests, with altitudes between 20 to 1,000 m a.s.l.. Average annual temperature varies from 18° to 20°C. Annual precipitation in the area is 1,500–2,200 mm (Ferraz and Varjabedian 1999). Our study site is located in an area of vegetation classified as submontane rain forest (Oliveira-Filho and Fontes 2000), and the altitude is between 714–837 m. The PECB, together with other adjacent conservation units, form one of the most important remnants of Atlantic Forest, containing more than 1,1 million ha. This is the only remaining Atlantic tract in which the whole assemblage of large carnivores has not been drastically disturbed, and still preserves the original conditions of this ecosystem.

*Nests search and observations* - Field work was conducted from September 2013 to February 2014, and from September to November 2014. We followed a complex of approximately 10 km of trails and streams in primary forest interior (~ 7 km of trails, and ~ 3 km of streams). Nests were located by chance, after all only females participate

in nesting activities and they do not exhibit territorial behavior. When we found nests, we described and photographed the nest, eggs, young, and nesting sites. We classified egg and nest shape according to Winkler (2004). We used a dynamometer scale (accurate to 0.1 g) to weigh the eggs, and a metal caliper (accurate to 0.1 mm) to measure nests and eggs. Nest materials were analyzed in details after fledging or predation.

We measured incubation period from the first day of incubation to the day before hatching, and nestling period from the hatching day to the day before fledging. Focal observations were conducted daily during laying phase so we could detect if incubation could begin before clutch completion. We never touched or handled the young to avoid shortening nestling period.

To estimate the proportion of time females spent incubating the eggs, as well as the frequency of feeding visits during nestling period, we performed focal observations of 1 hr per day using 8 X 40 binoculars, and we filmed the nests during these observations. These observations were always made early in the morning (06:00–10:00 hr).

We have assumed nest predation when eggs or nestlings younger than fledging age disappeared from a nest (Pletschet and Kelly 1990). We estimated probability of survival (nesting success) separately for incubation and nestling periods and for the whole nesting cycle (incubation plus nestling), using the method of Mayfield (1961). We used mean incubation and nestling period lengths as exponents to calculate the probability of nest success. Egg-laying stage was not considered. Descriptive statistics are presented as mean  $\pm$  SD (Standard Deviation).

## RESULTS

We analyzed 36 active nests, 15 in the 2013/2014 breeding season and 21 in 2014/2015 season. The earliest breeding activities were on 05 November 2013 (incubation), and 07 October 2014 (incubation). The latest nesting activities (the last young observed in a nest) were recorded on 04 February 2013 in the first season, and the second season is unfinished. Thus, breeding seasons ranged from November to February in 2013/2014 (Fig. 1).

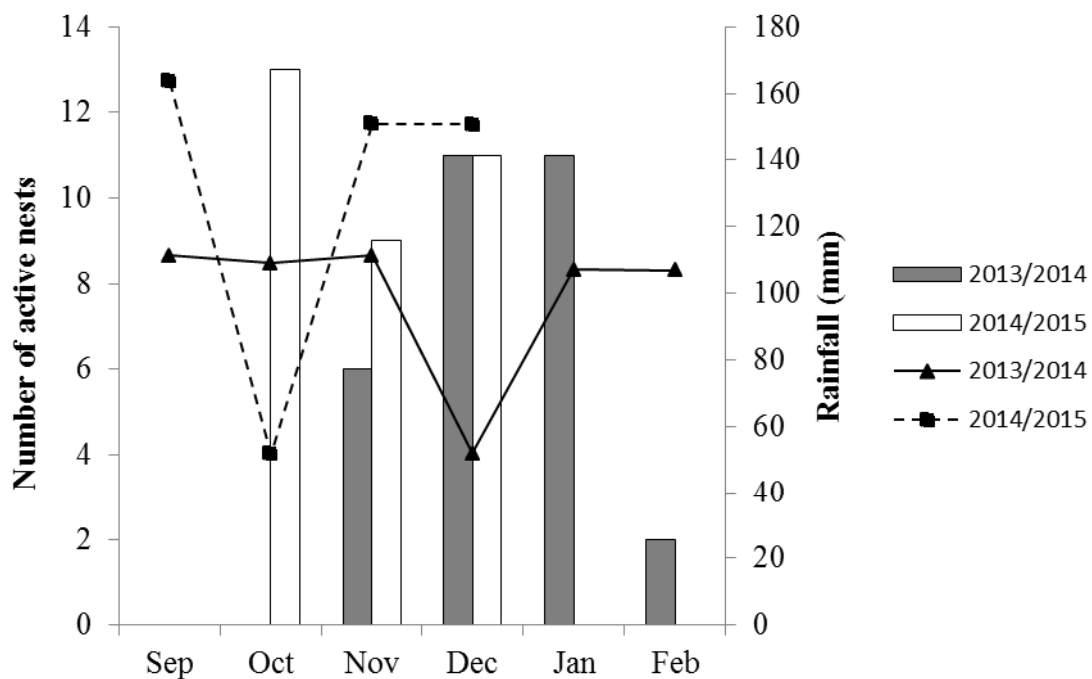


Fig. 1. Numbers of active nests (in incubation and nestling periods) per month during two breeding seasons (2013/2014 and 2014/2015), and total monthly precipitation.

Nests were simple and delicate cups, hanging from a horizontal fork, in thin branches of small trees or shrubs. They were attached to the twigs by fungal hyphae or spider web (Fig 2A-B). Nest material was mainly rachis of leaves, rootlets and thin vegetal fibers, stitched with black fungal hyphae, and had a dark brown general color. Sometimes tufts of green moss and dry or green leaves were used in the outside walls

(Fig 2B). Fine roots and fungal hyphae hung from the nest, forming a ‘tail’ underneath (Fig. 2C). Of 15 nests, 10 were built over the water and the others were placed 0–6 m from the margin of small forest streams. One nest observed from the very beginning was constructed in four days.



Fig. 2A. Nest attached to forks with fungal hyphae; B. Nest attached to forks with spider web; C. filaments hanging from the nest forming a ‘tail’.

Nest measurements were: outside diameter  $7.56 \pm 0.87$  cm (range = 6.92–9.05), inside diameter  $6.31 \pm 0.50$  cm (range = 5.94–7.21), outside height  $4.63 \pm 1.16$  cm (range = 3.81–6.99), inside height  $3.70 \pm 0.86$  cm (range = 2.66–5.15) ( $n = 13$ ), ‘tail’ length  $56.05 \pm 33.46$  cm (range = 7.82–125.0), and height of nest border above ground or water  $1.71 \pm 0.49$  m (range = 1.14–2.98) ( $n = 12$ ).

Eggs color pattern was highly variable. Background color varied from beige to light brown. Markings could be light or dark brown, and in some eggs they were pale.

In all of the eggs, large round or elongated blotches were concentrated in the large end, or formed a crown near the large end or towards the middle of the egg (FIG. 3A). Smaller spots were distributed all over egg surface and their densities were also highly variable among eggs. Egg measurements ( $n = 24$ , from twelve nests) were: length  $24.76 \pm 1.27$  mm (range = 23.2–28.5); width  $17.23 \pm 1.31$  mm (range = 16.1–21.6) and weight  $3.67 \pm 0.29$  g (range = 3.1–4.4,  $n = 8$ , from four nests). Clutch size was two eggs or young ( $n = 36$ ). In three nests eggs were laid on consecutive days and in three others they were laid with one day interval. Incubation started the morning the females laid the last egg ( $n = 8$  nests). During this stage, females spent 22:07–52:27 min incubating per hr ( $44:05 \pm 12.46$  min). They left the nests one to two times per hr ( $1.8 \pm 0.45$ ), and incubation recesses varied from 3:19–15:08 min ( $15:57 \pm 12.44$ ) ( $n = 21$  hr in 9 nests). Incubation period was 18 days (six eggs in three nests). Of ten nests observed in incubation stage ( $n = 20$  eggs) that reached nestling phase, we observe two infertile eggs. Hatching was not synchronous in only one of five nests.

Hatchlings showed dark-red skin and were covered with sparse dark gray down. The bill is ochre and swollen flanges were white, while mouth lining was yellow (Fig. 3B). Nestling periods were 16 days for four nestlings from two nests, and 15 days in a nest containing only one nestling. In 19 hr of observation at six nests, young were fed on average  $1.5 \pm 0.82$  times/h (range = 0–2) and only females fed the young. Females swallowed fecal sacs in six of seven observations, and dropped it far from the nest one time (Fig. 3C). Young left the nests with well-developed feathers, except in the head, and flying weakly (Fig. 3D).



Fig. 3A. Eggs of Blue Manakin; B. hatchlings; C. Fecal sac being expelled by a middle development stage nestling, and D. Nestlings in the day before fledging.

Nest survival was 65% during incubation (one predation and three abandonments in 163 nest days,  $n = 15$  nests), and 62% during the nestling stage (three predation events in 101 nest days,  $n = 9$  nests). Overall nesting success, from egg-laying to fledging, was 40% (264 nest days,  $n = 16$  nests).

## DISCUSSION

*Nest, eggs and nestling characteristics.*---Generally, swallow cups hanging by their rims in slender horizontal forks, built in bushes or saplings in forest understory is the pattern of Pipridae nests. However, nest material, color, and compactness is variable even within the same genus. The nests of Blue Manakin are quite similar to Long-tailed

Manakin, *Chiroxiphia linearis* (Foster 1976), except that in Long-tailed Manakin only 35% of the nests presented the tail of hanging materials underneath. In the latter, nest tails also were shorter (up to 8.5 cm) and mostly composed of entire dry leaves, while in Blue Manakin the tail was mostly composed of fibers. Although Yungas Manakin, *Chiroxiphia boliviana* is known from only one nest, it presented important differences: nest walls were built of beige grass fibers and rootlets, and dry bamboo leaves were used in the external layer, giving the nest a yellowish appearance. It also seems to be more compact, and tail was absent (Hazlehurst and Londoño 2012). This pattern is more similar to nests of Blue-crowned Manakin (Skutch 1969) than to other *Chiroxiphia*. Other patterns of piprid nests are, for instance, those presented by Cerulean-capped Manakin, *Lepidothrix coeruleocapilla* (Kirwan et al. 2011) and Green Manakin, *Cryptopipo holochlora* (Christian 2001), in which external layers and tail are mostly composed of green live moss, while the nests of White-bearded Manakin are simpler, more compact, and slightly deeper, built of rootlets and other flexible fibers, lacking any external adornment and tail (Snow 1962).

Nest placement over or near the water were also reported for Wire-tailed Manakin, *Pipra filicauda* (Hidalgo et al. 2008), Golden-winged Manakin, *Masius chrysopterus* (Greeney and Gelis 2007), White-bearded Manakin (Oniki and Willis 1983; Snow 1962), Green Manakin (Willis 1966, Christian 2001), Yellow-headed Manakin, *Chloropipo flavicapilla* (Kirwan and Green 2011), Orange-crested Manakin, *Heterocercus aurantiivertex* (Álvarez 2001), and Yungas Manakin. However, due to the limited number of nests analyzed or nest search methods, these studies did not permit to infer if these species have select water proximities as nesting sites. Here, as nests searches have been conducted near and far from water, our data suggest that Blue Manakin have selected streams proximities to reproduce.



The eggs of Blue Manakin were similar to the eggs of other *Chiroxiphia*, except for Yungas Manakin which background color was slightly lighter. Eggs background color also vary among other piprids, being grayish in Red-capped Manakin, *Ceratopipra mentalis* and Blue-crowned Manakin (Skutch 1969), tan in Helmeted Manakin, *Antilophia galeata* (Marini 1992), and olive in Golden-winged Manakin (Greeney and Gelis 2007), Green Manakin (Christian 2001), and Yellow-headed Manakin (Kirwan and Green 2011). However, these comparison must be viewed with caution because based on our own observations, there can be significant intraspecific variations in egg color, that could confound comparisons, especially if they are based on a limited number of nests. Nestlings described for the genus *Chiroxiphia* also present remarkable variations. Foster (1976) and Hazlehurst and Londoño (2012) describe the mouth lining of Yungas Manakin and Long-tailed Manakin as golden-yellow, while in Blue Manakin it was light yellow. Pink skin color, have been reported for Yungas Manakin and Red-capped Manakin (Skutch 1969), while in Blue-crowned Manakin (Skutch 1969) it was dark red like in Blue Manakin.

The family Pipridae is monophyletic and relationships among genera is well-resolved (McKay et al. 2010). Although nest architecture can be phylogenetically informative in some groups of Neotropical passerines (Greeney et al. 2013), here nest, eggs, and young characteristics varying within genera, e.g. *Lepidothrix* and *Chiroxiphia*, suggest that these traits are not diagnostic of genera and may not be informative to reconstruct phylogeny in this group.

*Breeding life history traits.*---Shorter breeding seasons in higher latitudes is a well-known phenomenon for Northern Hemisphere birds, especially in temperate latitudes (Hemborg et al. 2001, Cooper et al. 2005, Renner and McCaffery 2006), but this issue

has been poorly evaluated in the Neotropics mainly due to the lack of breeding phenology data across the vast Central and South American latitudinal gradient. Only recently, this pattern of variation has been demonstrated to occur in a Neotropical bird, the Pale-breasted Thrush, *Turdus leucomelas*, in which breeding season length in a Tropical/Subtropical population has been more than half of that found in equatorial populations (Davanço et al. 2013). This pattern also has been corroborated by observations between species of Neotropical thrushes distributed in different latitudes (Davanço et al. 2013), then we believe that interspecific comparisons of closely related species also may provide valuable insights on this subject. The breeding season found for Blue Manakin in our study area was shorter than the population studied by Foster (1977) in Paraguay (August to February), but it matched breeding season durations reported in other studies on piprids conducted in the Tropical region, e.g. Band-tailed Manakin, *Pipra fasciicauda*, in Mato Grosso do Sul, Brazil (four months; August to November) (Oniki and Willis 1983), and Helmeted Manakin, in Minas Gerais, Brazil (five months; August to December) (Marini 1992; Marini et al. 1997). On the other hand, in equatorial region breeding seasons were longer. For Blue-backed Manakin, *Chiroxiphia pareola* from Belém, Brazil, it lasted eight months (September to April) (Pinto 1953), and Long-tailed Manakin, from Costa Rica have reproduced all year round (Foster 1976). Breeding seasons of eight months were found for Crimson-hooded Manakin, *Pipra aureola* (October to May in Surinam and French Guiana) (Tostain 1988), and Red-headed Manakin (September to April in Belém, Brazil) (Pinto 1953). For White-bearded Manakin it lasted eight months in Surinam (August to March) (Snow 1962), and nine in Trinidad (January to September) and in Belém, Brazil (August to April) (Snow 1962; Oniki and Willis 1983). White-crowned Manakin, *Dixiphia pipra*, reproduced during ten months in French Guiana (August to May) (Tostain 1988).

These comparisons suggest that the Pipridae also conform the pattern of shorter breeding seasons in higher latitudes, and reinforces the findings that breeding season length adjustments in response to latitude also occurs in Neotropical passerines (Davanço et al. 2013). In temperate habitats breeding season length is often correlated to the number of broods per season, which is an important component of annual fecundity (Martin 1995, Sanz 1998, Cooper et al. 2005). Then, if longer breeding seasons in equatorial piprids translates into more broods per year remains an important open question for understanding fecundity across latitudes.

Piprids also were not consistent with the pattern of larger clutch sizes in higher latitudes observed in many temperate birds (Skutch 1949, Ricklefs 1980, Jetz et al. 2008), since all of the species and populations studied invariably presented clutches of two eggs (for review, see Snow 2004). Two alternative but non-excluding explanations could account for this pattern: first, piprids occur in rain forests that are mainly distributed in equatorial and tropical latitudes, not reaching harsh weather conditions that could select for larger clutch sizes. In Northern Hemisphere, certain species begin to present clinal clutch size variation only after 30°N (Dhondt et al. 2002), and the limit of the distribution of piprids in South America is 30°S (Ridgely and Tudor 1994). Second, hypotheses evoked to explain clutch size latitudinal variation have often been based on food limitation (Lack 1954, 1968; Ashmole 1963; Ricklefs 1980). Ashmole (1963) hypothesis, for instance, argue that clutch size increases with resources availability during the breeding season and decreases with increasing population density. Consequently, the harsh winter limiting population density in non-breeding season, and longer days permitting to gather more food during the breeding season would result in larger clutches in higher latitudes (Ricklefs 1980). Piprids, however, have primarily frugivorous diet, and the fact that fruits are abundant and conspicuous

resources in tropical forests is what has molded many aspects of their life history (Snow 1962, 1985). If this is true, clutch size variations in response to food limitation are not expected to occur in these birds.

The only incubation and nestling periods known for *Chiroxiphia* in the wild were cited by DuVal (2007) as unpublished data for Lance-tailed Manakin, *Chiroxiphia lanceolata* (18 and 16 days, respectively). For only one nest of Blue-backed Manakin in captivity incubation and nestling periods were 17 and 15 days. Periods of incubation are also described for Blue-crowned Manakin (17 and 19 days,  $n = 2$ ; Skutch 1969), Orange-collared Manakin (18–20 days, Skutch 1969), and White-bearded Manakin (18–19 days; Oniki and Willis 1983, Snow 1962). Nestling periods are described for Golden-headed Manakin (16–17 days, Tostain 1988), Red-headed Manakin (13–14 days, Pinto 1953), Blue-crowned Manakin (13–15 days, Skutch 1969), and Orange-collared Manakin (Skutch 1969), Golden-collared Manakin (Worthington 1982) and White-bearded Manakin (Oniki and Willis 1983; Snow 1962) with 13–15 days. These nesting cycles are similar to other Neotropical forest passerines, such as *Thamnophilidae* and *Formicariidae* (Skutch 1945, 1969), and generally, they have been thought to be long if compared to passerines from temperate habitats (Ricklefs 1976, Martin 1996, Martin 2002, Auer et al. 2007), while Geffen and Yon-Tov (2002), in a wide range study proved that they can be similar. As nest predation rates have been traditionally thought to be higher in the Neotropics (Skutch 1949, 1985; Robinson et al. 2000; Ryder et al. 2008), Martin (1996) has posed a paradox: why breeding cycle of tropical birds are so long if it increases time-dependent nest predation risks? Although an alternative hypotheses based on adult and juvenile mortality have been proposed to explain these findings (Martin 2002), our data did not corroborate the main assumption of this paradox, as nest predation rate was very low, even compared to northern

hemisphere studies (Skutch 1949, 1985; Oniki 1979; Martin et al. 2000; Robinson et al. 2000; Ryder et al. 2008). Our data is consistent with the early insights of Oniki (1979) that nest predation rates in the Neotropics could have been overestimated especially due to works conducted in disturbed or insular areas, e.g. White-bearded Manakin (81% in Trinidad, Snow 1985). Orange-collared Manakin (75% in Costa Rica, Skutch 1985), Red-capped Manakin (71%, Mayfield 88% in Panama, Robinson et al. 2000), and Wire-tailed Manakin and Blue-crowned Manakin (84%, being 11% abandonment, in Ecuador; Ryder et al. 2008). In disturbed habitats, populations of mid-sized, or mesopredators, which are the main nest predators, increases without control due to the rarity of large carnivores (mesopredator release hypothesis) (Terborgh 1974, Oniki 1979, Robinson and Sherry 2012), increasing nest predation rates. The, we suggest that the paradigm that nest predation rates are higher in the tropics should be better investigated (see also Martin et al. 2000).

In the Pipridae family, males are predicted not to provide parental care, which has been hypothesized to be possible due their frugivorous diet. According to Snow (1985), eating fruits do not demand much energy to forage and females can feed the young alone, permitting male desertion (Snow 1962, 1985). David Snow have proposed his theory mostly based on Pipridae and Cotingidae birds, but actually, parental care is poorly known in these birds. For the Red-ruffed Fruit-crow, *Pyroderus scutatus* (Cotingidae), for instance, male and female shared parental care (Francisco et al. 2008), while parental care data is absent for most piprids. In this work, the premise that only females provide parental care is corroborated.

## CONSIDERAÇÕES FINAIS

O ninho de *C. caudata* segue um padrão geral de ninhos de piprideos, porém existem diferenças na coloração e na robustez dos ninhos, mesmo entre espécies do mesmo gênero. Quanto a localização desses ninhos serem próximos à água, só foram reportados para *Pipra filicauda* (Hidalgo et al. 2008), *Masius chrysopterus* (Greeney & Gelis 2007), *Manacus manacus* (Oniki & Willis 1983; Snow 1962), *Xenopipo holochlora* (Willis 1966, Christian 2001), *Chloropipo flavicapilla* (Kirwan & Green 2011), *Heterocercus aurantiivertex* (Álvarez 2001), e *C. boliviana*. Porém como poucas metodologias de busca de ninhos são descritas, não podemos relacionar a localização dos ninhos com a proximidade da água. No nosso caso, os ninhos foram procurados tanto longe como perto da água, e portanto podemos inferir que *C. caudata* prefere locais próximos a riachos.

Os ovos das espécies do gênero *Chiroxiphia* parecem seguir um padrão, e os ovos de *C. caudata* o acompanha, e dentro da família a coloração do fundo do ovo pode variar de bege a oliva, passando por acinzentado. Os ninhegos do gênero *Chiroxiphia* possuem algumas variações, enquanto em *C. boliviana* e *C. linearis* apresentam a boca na coloração amarelo dourada (Hazlehurst & Londono 2012, Foster 1976), a boca de *C. caudata* é um amarelo claro, já a pela do ninhego ao nascer em *C. caudata* é vermelha escura e em *C. boliviana* é rosa (Hazlehurst & Londono 2012).

A variação da duração da temporada reprodutiva de acordo com a latitude é bem conhecida em ambientes temperados, porém isso é pouco conhecido para as espécies neotropicais (Hemborg et al. 2001, Cooper et al. 2005, Renner & McCaffery 2006). A temporada reprodutiva, acompanhada por nós, para *C. caudata* teve duração de quatro meses, três meses a menos do que a encontrada por Foster (1977) para uma população

da mesma espécie estudada no Paraguai. Em outras espécies da mesma família, estudadas em latitudes mais próximas a nossa, a duração foi muito parecida (de 4 a 5 meses), já para espécies equatoriais a duração da temporada foi maior (8 a 10 meses). Essa variação pode ser um indício de que há um ajuste na duração da temporada reprodutiva de acordo com a latitude também em espécies neotropicais. Geralmente os dados de duração de temporada reprodutiva estão relacionados ao número de ninhadas por temporada (Martin 1995, Sanz 1998, Cooper et al. 2005). Se essa maior duração da temporada em espécies equatoriais significa mais ninhadas por ano, é uma grande incógnita para se entender a fecundidade entre diferentes latitudes.

As espécies que compõem a família pipridae não seguem o padrão latitudinal de tamanho de ninhada observado em aves de regiões temperadas (Skutch 1949, Ricklefs 1980, Jetz et al. 2008), já que todas as espécies estudadas possuem tamanho de ninhada igual (2 ovos/filhotes por ninhada) (see Snow 2004). Isso pode ocorrer por dois motivos, por só ocorrerem em latitudes das regiões equatoriais e neotropicais, pode não haver variação climática suficiente para selecionar tamanho de ninhadas. Ou pela hipótese que busca relacionar tamanho de ninhada com limitação de recursos alimentares entre as latitudes (Lack 1954, 1968; Ashmole 1963; Ricklefs 1980). No entanto piprideos possuem grande parte da sua dieta baseada em frutos, e esses são dados como recursos abundantes em florestas tropicais (Snow 1985). Sendo assim, a limitação de alimentos não deve ser a causa da variação do tamanho de ninhada nessas aves.

Os períodos de incubação e de ninhegos encontrados para piprideos, seguem um padrão próximo ao observado em outros passeriformes florestais neotropicais como *Thamnophilidae* e *Formicariidae* (Skutch 1945, 1969), que tendem a ser considerados longos em comparação aos passeriformes de ambientes temperados (Ricklefs 1976,

Martin 1996, Martin 2002, Auer et al. 2007). As taxas de predação são reconhecidamente consideradas altas em ambientes neotropicais (Skutch 1949, 1985; Robinson et al. 2000; Ryder et al. 2008), porém nossos dados mostram taxas de predação baixas se comparados a trabalhos realizados no hemisfério norte (Skutch 1949, 1985; Oniki 1979; Martin et al. 2000; Robinson et al. 2000; Ryder et al. 2008). Podemos considerar assim, que as taxas de predação nos Neotrópicos podem ter sido superestimadas muito possivelmente por estudos realizados em áreas degradadas (Oniki 1979), exemplos são: *M. manacus* (81% em Trinidad; Snow 1985). *M. aurantiacus* (75% na Costa Rica; Skutch 1985), *C. mentalis* (71%, Mayfield 88% no Panamá; Robinson et al. 2000), e *P. filicauda* e *L. coronata* (84%, sendo 11% por abandono, no Ecuador; Ryder et al. 2008). De acordo com a hipótese de “libertação de mesapredadores” em áreas perturbadas, as populações de predadores de topo podem ser muito pequenas ou nem existirem e assim, a de mesopredadores, que são os principais predadores de ninhos, aumenta por não estar sendo controlada pelos grandes carnívoros (Terborgh 1974, Oniki 1979, Robinson & Sherry 2012).

De acordo com a teoria proposta por Snow (1985), em aves frugívoras, como os componentes da família Pipridae, não é esperado que os machos participem do cuidado parental, pois a dieta frugívora requer menor esforço para o forrageio, gastando assim menos energia, portanto as fêmeas conseguem cuidar da prole sozinha, permitindo que o macho abandone os cuidados referentes ao ninho sem arriscar perder seus filhotes. Em contrapartida o Pavó, *Pyroderus scutatus* (Cotingidae), tanto o macho quanto a fêmea participam do cuidado parental (Francisco et al. 2008). Nossos dados corroboram essa teoria proposta por Snow (1985) onde apenas as fêmeas são responsáveis pelo cuidado parental.



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