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IT'S NOT EASY BEING GREEN: USING MOLT AND MORPHOLOGICAL CRITERIA TO AGE AND SEX GREEN-PLUMAGE MANAKINS (AVES: PIPRIDAE)

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Resumen. – No es fácil ser verde: El uso de criterios morfológicos y patrones de muda para determinar el sexo y la edad de saltarines con plumaje verde (Aves: Pipridae). – La habilidad para determinar la edad y el sexo de aves puede contribuir con estudios que abarcan desde demografía poblacional hasta biología reproductiva. El sexo y la edad de las aves que se reproducen y migran a lo largo de Europa y Norte América se determinan comúnmente en base a patrones de muda. Sin embargo, hasta la fecha no se ha desarrollado una aproximación similar para las aves que anidan en latitudes tropicales. En este estudio, hemos desarrollado una técnica para determinar la edad y el sexo de saltarines con plumaje verde (Pipridae). Mediante el uso de técnicas comúnmente utilizadas para aves paserinas de áreas templadas, se determinó la edad de 108 individuos y el sexo de 41 individuos de tres especies de saltarines: Saltarín Coroniazul (*Lepidotrix coronata*), Saltarín Coroniblanca (*Pipra pipra*), Saltarin Cola-de-Alambre (*Pipra filicauda*). Las aves que eclosionaron el año de la captura (HY) se diferenciaron de las que eclosionaron en años anteriores (AHY) debido a la retensión de algunas cobertoras mayores y/o cobertoras primarias de estadios juveniles. Las aves que completaron su muda prebásica y que no mostraron ningún otro signo de plumaje masculino fueron clasificadas como hembras. El sexo de los individuos con vestigios de plumaje masculino no fue determinado con precisión, debido a que las hembras de mayor edad pueden poseer algunos atributos de plumaje masculino. Las técnicas para determinar el sexo fueron validadas mediante el uso de técnicas moleculares y probaron ser altamente confiables. Hasta la fecha, no tenemos suficientes datos de recapturas para evaluar detalladamente las técnicas de determinación de edad de individuos con plumaje verde. Sin embargo esta técnica demostró ser precisa para machos capturados en las asambleas de cortejo. Consecuentemente, las técnicas de determinación de edad y sexo presentadas en este artículo constituyen una contribución útil para el entendimiento de la variación de la supervivencia, demografía poblacional y éxito reproductivo.

Abstract. – The ability to age and sex individual birds can enhance studies ranging from population demographics to reproductive biology. Birds that breed and migrate through Europe and North America are commonly aged and sexed based on molt patterns. Yet to date, a similar approach has not been developed for birds breeding at tropical latitudes. Here we develop a technique for aging and sexing green-plumage manakins (Pipridae). We aged 108 individuals and sexed 41 individuals of three species, Blue-crowned Manakin (*Lepidothrix coronata),* White-crowned Manakin *(Pipra pipra)*, and Wire-tailed Manakin (*Pipra filicauda*), with techniques commonly used for temperate passerines. Hatching-year birds (HY) were distinguishable from after-hatching-year birds (AHY) by retention of some juvenile greater coverts and/or juvenile primary coverts. Birds which had completed their second prebasic molt and had no signs of male plumage were sexed as female. Individuals with signs of male plumage were not reliably sexed because old females can attain some attributes of male plumage. The sexing technique was validated using molecular

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techniques to determine sex and proved highly accurate. To date we have insufficient recapture data to thoroughly evaluate the aging techniques for green plumage individuals. However, it has proven accurate for males captured at leks. Thus, the sexing and aging techniques presented here constitute a useful addition to understanding variation in survival, population demographics, and reproductive success. *Accepted 3 June 2005*.

Key-words: Aging, manakins, molt, molecular sexing, Pipridae, tropical birds.

INTRODUCTION

Age-class structure and detailed population demographics are essential components of avian ecology because they provide insight into population level processes. Moreover, age class is an important confounding variable in many studies of avian biology yet, to date, population age structure remains underappreciated (Mulvihill 1993). A poor understanding of population structure and, therefore, population demographics among birds can hinder our ability to understand variation in survival, habitat use, and reproductive success. In the absence of detailed mark-recapture studies, it can be difficult to age and sex individuals in the field for species that lack sexual dimorphism and/or where juveniles have delayed plumage maturation and remain in female-type plumage for extended periods. Thus, development of field tools for aging and sexing birds in the hand can provide needed age data in a more time efficient manner.

Differentiation of young passerines from adults through use of plumage criteria can be attributed to Dwight (1900). Contemporary studies on temperate passerines (e.g., Mewaldt 1958, Foster 1967, Bancroft & Woolfenden 1982, Lloyd-Evans 1983, etc.) have contributed to the early finding of plumage differences among age classes of birds. The use of molt patterns for aging and its broad implementation in the current temperate ornithological sphere was furthered by Jenni & Winkler (1994) in Europe, and Mulvihill (1993) and Pyle (1997) in North America. However, plumage differences among age classes of tropical birds remain poorly known and infrequently studied.

The study of molt in temperate passerines provides a sound framework for understanding variation in patterns of feather replacement among tropical species. In most passerines, immature or juvenile birds undergo a partial first prebasic molt approximately one to two months after leaving the nest which includes body feathers, lesser coverts, median coverts, a variable number of greater coverts and less commonly tertials, but excludes primary coverts, remiges and rectrices (Mulvihill 1993, Pyle 1997, Pyle *et al.* 1997). In contrast, adults ordinarily have a complete prebasic molt which includes all body feathers, coverts, rectrices and remiges (Mulvihill 1993, Pyle 1997, Pyle *et al.* 1997). The partial nature of the first prebasic molt in hatching-year (HY) birds means that birds display two "generations" of feathers because of the retention of outer greater coverts and primary coverts (Mulvihill 1993, Pyle 1997). Moreover, retained juvenile feathers typically have lower barb density and tend to be shorter than replaced coverts (Ryder, pers. observ.). Boundaries between retained and replaced wing coverts are termed "molt limits" and can be used to differentiate HY birds from AHY birds (i.e., adults) (Mulvihill 1993, Jenni & Winkler 1994, Pyle 1997). Techniques used for aging temperate passerines may also be applied to those tropical families or species in which molt sequences follow known patterns.

Manakins are sub-oscine passerines in the

New World family Pipridae and are found in warm humid regions from Central to South America (Hilty & Brown 1986, Ridgely & Tudor 1994). Manakins are small understory and sub-canopy birds characterized by short tails, chunky build and small bills (Hilty & Brown 1986). Most species are well known for their sexual dichromatism in which males are boldly patterned whereas females are dull olive or green (Hilty & Brown 1986, Ridgely & Tudor 1994). A few brightly colored feathers can be found in the crown, nape and auricular region of adult females of many *Pipra* species (Graves 1981), although further study is needed to document the frequency of such a phenomenon in the genera.

Adult manakins, as in most other passerines in both temperate and tropical regions, undergo a complete molt after breeding (Snow 1962a, 1962b, 1976; Poulin *et al.* 1992, Ralph & Fancy 1994, Marini & Durães 2001, Snow 2004). In contrast, immature birds replace plumage in a prolonged partial molt that consists of head and body, lesser coverts and some inner greater coverts resulting in a female-type plumage in both sexes (Snow 1962a, 1962b, 2004). The age at which males attain definitive plumage may vary from two to four years; however only a few species have been studied in detail (e.g., Lill 1976, Foster 1987, McDonald 1993; Snow 1962a, 1962b, 2004) and accurate age data was lacking from earlier work. Thus, the presence of delayed plumage maturation among males has complicated detailed field studies of this family (Anciães and Del Lama 2002).

Our inability to age and sex green-plumage manakins makes them ideal candidates for using our knowledge of molt from temperate systems. We first describe the plumage sequence for Wire-tailed Manakin (*Pipra filicauda)*, White-crowned Manakin (*Pipra pipra)* and Blue-crowned Manakin (*Lepidothrix coronata)*. We next describe a technique for aging and sexing green-plumage manakins. Using common techniques for temperate passerines, we developed molt criteria for differentiating HY birds from AHY birds and a method for determining which green-plumage individuals are females. We tested the accuracy of our sex differentiation using molecular techniques. Finally, we investigate the use of morphological data to predict the sex of individual Wire-tailed Manakins.

METHODS

This research was conducted at Tiputini Biodiversity Station (TBS) (00º38´S, 76º08´ W), located along the Tiputini River in the Orellana Province of eastern Ecuador. This 650-ha biological station is located ~200 m above sea level, adjacent to Yasuní National Park and within the greater Yasuní Biosphere Reserve. The vegetation is a combination of *terra firme*, várzea and igapó lowland wet evergreen forest with a canopy height of 20–40 m (Nabe-Nielsen 2001). The climate is aseasonal with rainfall ranging from 100 to 600 mm monthly with periodic precipitation deficits and an average temperature of 28°C (Nabe-Nielsen 2001).

We used ground-level mist nets (12.5 m x 2.8 m, 36-mm mesh) to capture manakins from June 2002 to August 2002 and from January 2003 to March 2004. Mist nets, despite certain biases (Karr 1981, Remsen & Parker 1983, Remsen & Good 1996), effectively sample understory birds of the size being studied here (Karr 1979, Levey 1988, Blake *et al.* 1990). Nets were opened as needed at different locations to maximize the number of individuals captured.

Captured manakins were weighed, sexed, aged, and banded with aluminum and individual color band combinations. Additionally, detailed morphological data (i.e., wing chord (WING), tail (TL), tarsus (TAR) and culmen length (CUL), bill width (WID) and depth (DEP), and body mass (WT)) were collected

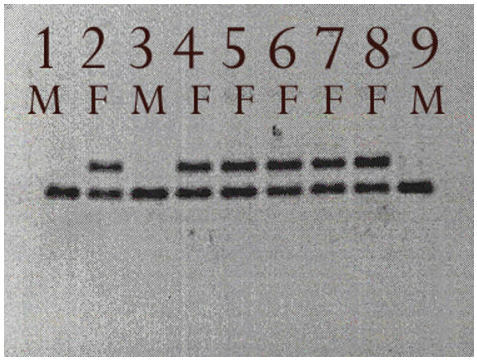

FIG. 1. Agarose gel showing one band for males and two for females after PCR amplification with the P2 and P8 primers.

for Wire-tailed Manakins. Blood samples were taken (~ 50 µl per individual) via puncture of the brachial vein. All blood samples were mixed with 500 µl of lysis buffer (100 mM Tris pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire *et al.* 1988).

Individual manakins in green plumage were aged by examination of the greater and primary coverts. Based on previous observations that immature manakins undergo a partial prebasic molt, we expected individuals less than one year old (i.e., HY birds) to show a molt limit within the greater coverts or between the greater and primary coverts and AHY birds to have uniform coverts. AHY individuals without molt limits (i.e., having completed two pre-basic molts) and without signs of male plumage were sexed as females. HY individuals were not assigned sex because the second prebasic molt in which attributes of definitive male plumage are gained had yet to be completed. Individuals that showed signs of male plumage (e.g., extensive red head feathers and/or black body feathers in the case of Wire-tailed Manakin) without molt limits were sexed as young males.

DNA was obtained via standard phenol-chloroform extraction method followed by a cleaning step of dialysis in 1X TNE_2 (10 mM Tris-HCl, 10mM NaCl, 2 mM EDTA). The concentration and integrity of extracted DNA was determined using spectrophotometry to examine DNA/protein ratios and then verified through electrophoresis by running samples on 0.8% agarose gels in 1X TBE. Following extraction and concentration verification, all genomic DNA was diluted to working concentrations of 20 ng/µl for purposes of uniformity. All individuals were sexed by running a standard PCR reaction using the P2 and P8 primers with annealing temperature set at 54ºC (Griffiths *et al.* 1998). Following the PCR reaction a digestion enzyme (Hae III) was added to all samples and left to incubate at 37ºC overnight. The samples were run on a 0.8% agarose gel for one hour and stained using ethidium bromide (EtBr). Males and females are differentiated because males show one band and females two (Fig. 1).

All morphological variables were checked for normality and homoscedasticity prior to data analysis; no transformations were necessary to meet the assumptions of parametric tests. We examined the ability of morphological variables to differentiate males and females using step-wise discriminant analysis (DA). DA seeks to extract underlying gradients of variation in which such variation is maximized among sample groups (McGarigal *et al.* 2000). We used two classification function techniques to determine misclassification rates and to predict group membership for individuals of unknown status. First we used classification functions for unequal sample sizes and second we used squared Manhalanobis distance to the centroid. Both classification techniques yielded identical prediction of group membership. We tested for differences among predictive variables defined by the DA using Wilk's lambda in a univariate analysis of variance (ANOVA) *F*-test. All statistical tests were conducted using SPSS, Version 11.0.1 (SPSS 2001).

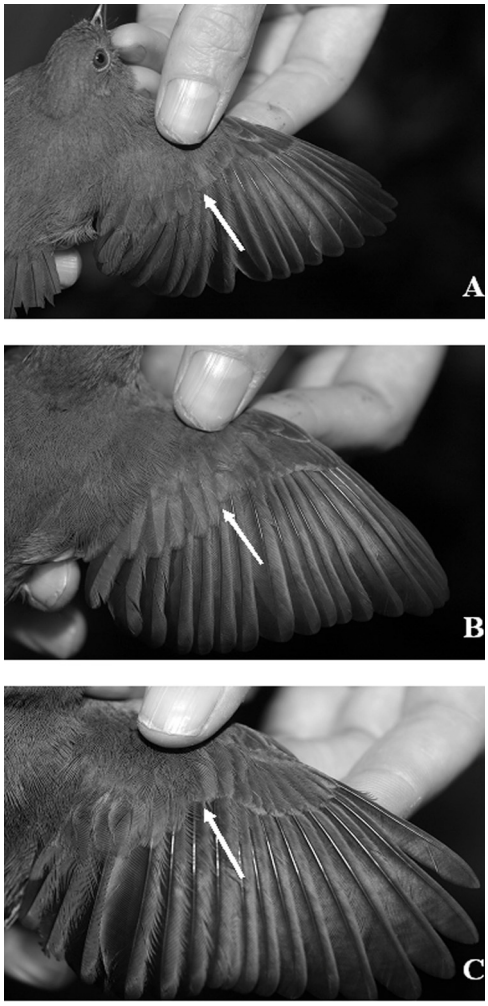

FIG. 2. HY manakins showing molt limits in the outer greater coverts as marked by white arrows. Retained juvenile outer greater coverts are identified by differences in color, wear, shape, length and barb density. A) Blue-crowned Manakin (*Lepidothrix coronata),* B) Wire-tailed Manakin (*Pipra filicauda),* C) White-crowned Manakin (*Pipra Pipra*).

RESULTS

Plumage sequence. Based on captures and recaptures of individual males at and around leks we have determined the plumage sequence for Wire-tailed Manakin, White-crowned Manakin and Blue-crowned Manakin. All three species follow the same pattern which may be generalized across the family once more data are available. Juveniles fledge the nest in a juvenile plumage which, in all three species, is green much like females. However, color intensity and shade appear duller in juveniles (Blake & Loiselle pers. com.) It appears that juvenile individuals undergo the first prebasic molt within two months of leaving the nest. This first molt consists of body plumage replacement as described above but includes no replacement of rectrices or remiges and results in molt limits within the coverts. During this molt, young males may acquire some signs of definitive plumage but frequency appears to be species specific. The second prebasic molt occurs at the end of the first breeding season or approximately 1 year after the first prebasic. This molt is complete and, in all three species, young males typically acquire significant signs of definitive male plumage (i.e., both head and body coloration). However, some young White-crowned Manakin males complete the second prebasic but still appear to show no signs of definitive male plumage (see discussion). Females that complete the second prebasic molt remain green but no longer show molt limits within the wing coverts. It is in the third prebasic molt that individuals acquire full definitive male plumage.

Sexing and aging in hand. Across the sampling period 108 green plumage manakins were captured (White-crowned Manakin, n = 37; Wire-tailed Manakin, n = 20; Blue-crowned Manakin, n = 51). Of those, 57 were aged as HY individuals that had completed one prebasic molt but had retained a variable number of greater coverts and/or primary coverts resulting in molt limits (Fig. 2). The remaining 51 individuals were aged as AHY individuals that had completed at least two prebasic molts

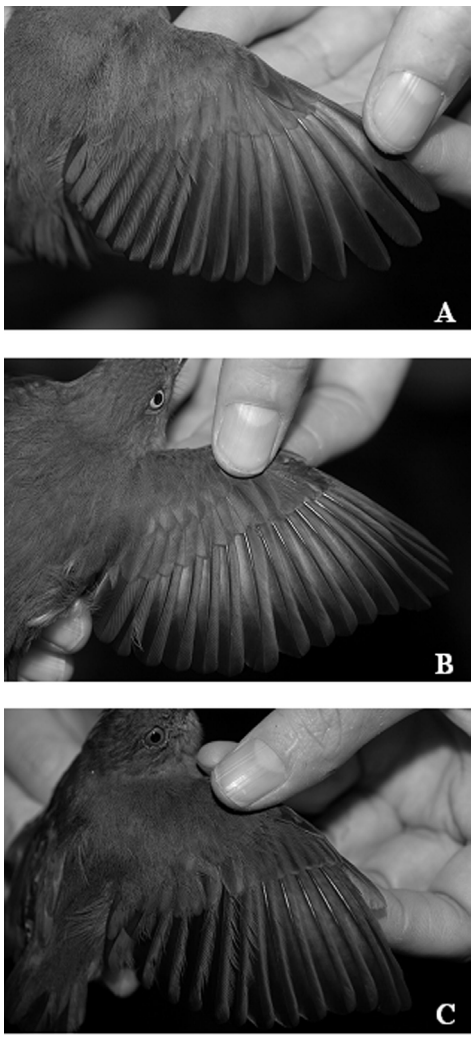

FIG. 3. AHY manakins that have completed two prebasic molts and thus, show uniform greater and primary coverts. A) Blue-crowned Manakin (*Lepidothrix coronata),* B) Wire-tailed Manakin (*Pipra filicauda*),C) White-crowned Manakin (*Pipra Pipra*).

resulting in uniform feather color and wear (Fig. 3). Of the individuals aged as AHY, we sexed 41 as females due to lack of molt limits and no signs of male plumage. Two individuals aged as AHY remained unsexed due to the presence of male colored plumage in the head. Eight other individuals were excluded from the analysis because blood samples had not been obtained making sex verification impossible.

Sex and age accuracy. Of the 41 individuals sexed as female in the field, 36 (88%) were confirmed as females in the lab using sexing primers. Four of the five mistakes were White-crowned Manakins and the fifth was a Wire-tailed Manakin. The Wire-tailed individual was sexed as female despite having two red head feathers (see discussion). To determine the accuracy of our aging technique, capture-recapture data between years is essential. Although we do not have such data from individuals used in this study, other individuals captured outside of the sampling period provide confirmation of the technique. On two occasions, males assigned HY status (i.e., molt limit with none to several colored head feathers) have been captured in the subsequent year in second year (SY) type plumage (i.e., mixed body plumage and multiple colored head feathers), and ultimately re-sighted or captured in definitive adult plumage in their third year. We have recorded two other occasions of individuals captured in SY type plumage and captured the following year in definitive male plumage. Further, no instances of captures assigned HY had been captured in previous years providing circumstantial evidence that their age categorization was correct. However, sample sizes to date preclude our ability to rigorously test the technique; its accuracy appears substantiated by our limited data.

Morphology. We used detailed morphological data from 157 Wire-tailed Manakins of known age and sex classes to determine if specific measurements could act in complementary and/or in substitution of the aging and sexing technique based on plumage. Morphology was predictive of both age and sex

TABLE 1. Morphological measurements (mean ± STD) for HY and AHY Wire-tailed Manakins (*P. filicauda*).

	Hatching Year (HY)	After-hatching year (AHY)	*P*
Wing (mm)	61.95 ± 1.42	63.73 ± 1.09	0.0001
Tail (mm)	52.47 ± 11.71	74.59 ± 9.15	0.001

TABLE 2. Tail (mm), weight (g) and bill depth (mm) measurements (mean ± STD) for male and female Wire-tailed Manakins (*P. filicauda*).

	Females	Males	*P*
Tail	56.27 ± 11.65	77.11 ± 5.50	0.0001
Weight	15.47 ± 1.45	13.75 ± 4.21	0.0001
Bill depth	3.75 ± 0.17	3.59 ± 0.17	0.0001

class but predicted the latter with greater accuracy. The discriminant function (D) was accurate in predicting age class in 140 of 157 (89.2%) of individuals [D = -26.628 + 0.321 (WING) + 0.086 (TL); (AHY > -0.941> HY)]. Differences among age classes were accounted for by AHY individuals having significantly longer wings ($F_{1, 155} = 41.255$, $P < 0.0001$) and tails ($F_{1, 155} = 90.816$, $P < 0.001$) (Table 1). The discriminant function correctly sexed 147 of 157 (93.6%) individuals captured in mist nets and sexed using molecular markers [D = 2.855 + 0.104 (TL) + -2.622 (DEP) + -0.069 (WT); (female < -0.917 < male)]. The function was more accurate at identifying males (94.6%) than females (88.9%). Sexes differed in all morphological variables except tarsus. The greatest proportion of the variance between the sexes was explained by males having a longer tail ($F_{1, 155} = 182.99$, $P < 0.0001$), females weighing more ($F_{1, 155} = 39.53$, $P = 0.0001$) and females having a greater bill depth ($F_{1, 155} = 17.59$, $P < 0.0001$) (Table 2, Fig. 4). We further tested the accuracy of the discriminant functions ability to classify individuals by using it to sex 16 individuals of unknown sex. The function correctly identified 11 of 16 (69%) of the unknown individuals later sexed with molecular techniques.

DISCUSSION

This study applied molt criteria widely accepted for aging birds in temperate regions to three species in the family Pipridae. Molt patterns were similar among the three species and followed the sequence previously described by Snow (1962a, 1962b, 2004). All three species retained some greater and or primary coverts after their first pre-basic molt resulting in molt limits. Thus, we differentiated HY birds from AHY birds by the presence of multiple ages of feathers in the coverts. This technique will likely be applicable to any tropical species in which the first prebasic is partial.

We further applied our knowledge of age criteria and plumage sequence to reliably sex green plumage individuals. Individuals that had completed two prebasic molts and still remained without signs of male plumage were reliably sexed as females. However, because older adult female manakins can acquire male plumage attributes, especially brightly colored head feathers (Graves 1981), some individuals without molt limits and signs of male plumage should be sexed with caution. On average, young males in their second year have much more extensive signs of male plumage (i.e., brightly colored head feathers and some black body plumage) (Ryder pers. observ.). However, the extent of male plumage acquired during the second prebasic molt appears highly variable both within and across species. For example some males may attain signs of definitive plumage after the first prebasic while other individuals may not attain any signs of male plumage until their third prebasic molt. As such, one source of error in our sexing appeared because a number of second

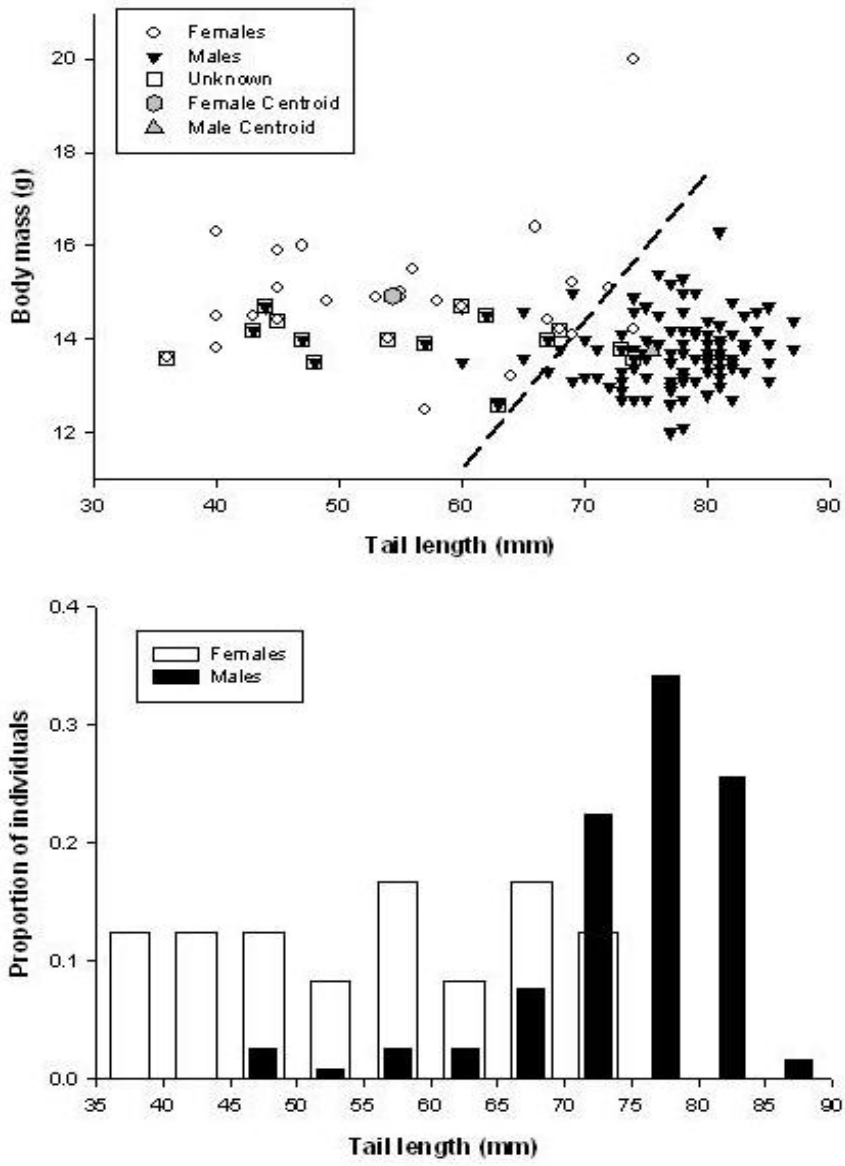

FIG. 4. A) Wire-tailed Manakin (*P. filicauda*) males and females differ in tail length and body mass. B) The distribution of tail lengths for males and females shows substantial overlap despite its explanatory power.

year male White-crowned Manakins had yet to attain any signs of male plumage. Alternatively, these individuals may have been incorrectly aged. Given that individual variation in plumage maturation occurs due to a number of intrinsic and extrinsic factors, it seems probable these rogue individuals were just late bloomers. Likewise, a female Wire-tailed

Manakin was misclassified as a second year male due to the presence of red head feathers. Clearly, further study on plumage variation among age and sex classes is needed within the family Pipridae.

The ability to combine the current techniques with morphological data is also promising given the example of Wire-tailed Manakin. Our data suggest we can further increase our predictive power to determining a green plumage individual's sex by combining techniques. Morphological data were able to correctly classify a high percentage of individuals. The predictive power of morphology alone, however, was low when trying to classify individuals at the extremes of the morphological measures distribution (i.e., females with long tails and males with short tails). These individuals in the extremes of morphological distribution were HY individuals, and point to the difficulty of sexing some age classes. Despite the inability of these techniques to classify all individuals in the field, they provide a major step forward for aging and sexing manakins.

Previous studies have described the plumage sequence for several species of manakins (e.g., Snow 1962a, 1962b, Lill 1976, Foster 1987, McDonald 1993). It has been reported that many male manakins attain definitive plumage at the beginning of their second year of life (Lill 1976, Castro-Astor *et al.* 2004). We do not challenge the accuracy of such a statement but rather we believe that plumage sequence based on only recapture data in which individuals were not aged should be taken with a caveat. It was recently reported that Red-headed manakin males attain definitive male plumage over a period of three to thirteen months (Castro-Astor *et al.* 2004). This finding suggests both individual variation in plumage maturation rate and that males attain definitive plumage before or during their second year of life. However, individuals were not aged at first capture making knowledge of the age which definitive plumage was attained impossible. The Red-headed manakin data do however give in-depth information into the length of time between plumage categories and may likely further point out variation in the plumage maturation rate of young males such as the White-crowned Manakins described here.

Our data for three species of Amazonian manakins suggest a three, rather than two, year pattern in which males attain definitive plumage during the third prebasic molt. Examples of *Chiroxiphia* manakins (e.g., Foster 1987, McDonald 1993) attaining definitive plumage in their fourth and fifth years have been described as anomalies for the manakin family. Our data suggest young male manakins may regularly delay plumage maturation into their third year and that those species which potentially attain definitive plumage in their second year may be exceptions to familial patterns in Pipridae. We further suggest that more detailed age specific studies should be conducted on all members of the family to better understand idiosyncrasies of molt patterns and plumage maturation. Furthermore, investigation of the relationship between plumage maturation and the social dynamics of variable lekking styles may shed light on factors driving delayed plumage maturation.

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