

## AGE DETERMINATION OF AMETHYST-THROATED HUMMINGBIRD (*LAMPORNIS AMETHYSTINUS*) AND WHITE-EARED HUMMINGBIRD (*HYLOCHARIS LEUCOTIS*)

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**Abstract** · Age is one of the most important parameters in avian biology, since life-history strategies and population dynamics can be strongly influenced by age. Two characters are generally used to age hummingbirds (family Trochilidae): presence of maxillar striations and presence of beige to cinnamon fringes of dorsal feathers in the juvenile plumage. However, their applicability varies among species. For this reason, development and use of species specific criteria are highly recommended. Here, we describe age- and sex-dependent variation of the central rectrix shape in Amethyst-throated Hummingbird (*Lampornis amethystinus*) and White-eared Hummingbird (*Hylocharis leucotis*). Juvenile central rectrices are more pointed than definitive ones. This criterion meets three crucial properties of aging techniques: high discriminant ability (78% for Amethyst-throated Hummingbird and 99% for White-eared Hummingbird), wide temporal applicability, and ease of use with minimum experience.

**Resumen** · Determinación de la edad del Colibrí Garganta Amatista (*Lampornis amethystinus*) y del Zafiro Oreja Blanca (*Hylocharis leucotis*)

La edad es uno de los parámetros más importantes en el estudio de la biología de las aves, ya que tanto las estrategias vitales como la dinámica de poblaciones pueden estar fuertemente influenciadas por la edad. La edad de los colibríes (familia Trochilidae) se determina generalmente mediante dos caracteres: presencia de estrías maxilares y presencia de márgenes beige o canela en las plumas dorsales del plumaje juvenil. Sin embargo, su aplicabilidad varía entre especies. Por esta razón el desarrollo y empleo de criterios específicos adquiere relevancia. En este artículo describimos la variación en función de la edad de la forma de la rectriz central en el Colibrí Garganta Amatista (*Lampornis amethystinus*) y en el Zafiro Oreja Blanca (*Hylocharis leucotis*): las rectrices centrales juveniles son más puntiagudas que las rectrices definitivas. Este criterio reúne las tres propiedades cruciales que deben poseer las técnicas de determinación de la edad: capacidad discriminante elevada (78% en el Colibrí Garganta Amatista y 99% en el Zafiro Oreja Blanca), amplia aplicabilidad temporal y facilidad de uso con una experiencia mínima.

**Key words:** Aging techniques · Circular statistics · Mexico · Neotropical hummingbirds · Plumage traits · Rectrix morphology

### INTRODUCTION

Age is one of the most important parameters in avian biology: reproductive performance (Curio 1983), molt strategy (Jenni & Winkler 1994), migration behavior (Newton 2008), and population dynamics (Lande et al. 2003) are strongly influenced by age. In North American hummingbirds, for example, age has a strong effect on dominance and territoriality (Ewald 1985, Carpenter et al. 1993) with potential consequences on survival and reproduction. Age determination in hummingbirds (family Trochilidae) is complicated by their small size since the smaller the species the harder to handle and to evaluate individual traits in field conditions; moreover, their iridescent plumage makes even more difficult to detect differences in color saturation and hue outside glittering patches, and particularly on wing coverts (pers. observ.), which allow to identify feather generations in passerines (i.e., paler and drabber juvenile versus darker and brighter formative/definitive feathers; Pyle 1997). Incomplete information about basic life-history traits and specific detailed molt descriptions for most Neotropical hummingbird species adds further complications, since it limits the use of techniques commonly applied to aging passerines, such as presence of molt limits and wear of flight feathers (Pyle 1997, Guallar et al. 2009).

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Despite these gaps of knowledge, two general characteristics of the ontogenetic process of hummingbirds are instrumental to age them: presence of maxillary striations (Ortiz-Crespo 1972) and presence of beige to cinnamon margins of dorsal feathers in the juvenile plumage (Ridgway 1911, Weller 2011). These characters are apparently common to all hummingbird species (Schuchmann 1999), and therefore can be considered as general aging criteria. Temporal applicability (i.e., the span during which it is valid) and discriminant ability are the most important properties of aging criteria to assess their validity (Peris-Álvarez 1983, Yanega et al. 1997, Guallar et al. 2009). Pale margins of juvenile feathers of hummingbirds are ephemeral and can be confusing in species with pale margins in definitive plumage, such as the White-eared Hummingbird (*Hylocharis leucotis*). Bill striation provides a powerful criterion during several months, as long as corrugations are easily observed and spread along a high percentage of the bill. Furthermore, it is known that adult hummingbirds retain striations at the bill's base (Ortiz-Crespo 1972), which limits the applicability of this criterion to a threshold of 10% striations (Yanega et al. 1997). Finally, bill striations can be very subtle and it is rather hard to estimate their percentage, especially in final stages.

Limitations of the general aging criteria may be overcome by the development of species-specific aging criteria. Feather shape, especially of rectrices and remiges, is a general aging criterion used to age passerines (e.g., Samson 1974, Laaksonen & Lehtikoinen 1976, Svensson 1992, Pyle 1997). This technique has wide temporal applicability since it can be used until remiges and/or rectrices are replaced, i.e. the whole first annual cycle. Discriminant ability of flight feather shape is high in passerines, particularly rectrix shape (Morris & Bradley 2000); however, it varies among species and must be used with caution (Balph 1977, Jackson 1992). Feather shape has also proven to be very useful for aging and sexing North American hummingbirds (Stiles 1972, Baldrige 1983; Baltosser 1987, 1994; Pyle 1997).

Amethyst-throated Hummingbirds (*Lampornis amethystinus*) and White-eared Hummingbirds have highly sexually dichromatic definitive plumages although they do not have evident sexual size dimorphism (Howell & Webb 1995). First-cycle individuals of these two species are sexually monochromatic but start acquiring sexual ornaments as they molt body feathers (Pyle 1997). However, they retain juvenile remiges and rectrices for up to 12 months in Amethyst-throated Hummingbird (eight in White-eared Hummingbird) before the onset of the first prebasic molt (unpubl. data; terminology based on Howell et al. 2003). This delay can potentially be used as aging criterion. Here, we describe age and sex-dependent variation of rectrix shape in a western Mexican population of these two Neotropical hummingbirds, and, for the first time in hummingbirds, assess its discriminant ability.

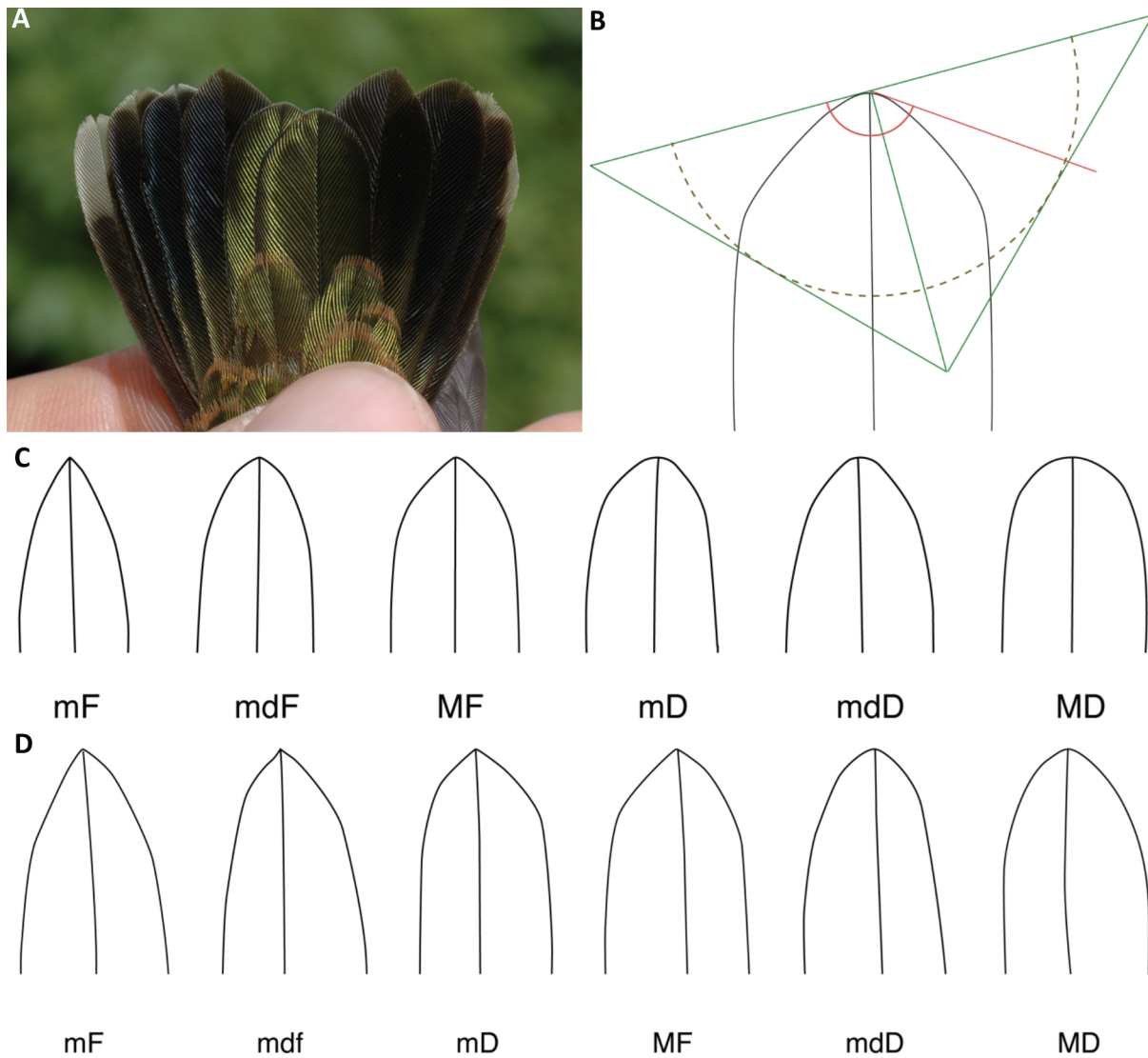
## METHODS

To quantify rectrix shape, we measured pointedness of the central rectrix (R1 hereafter) on photographs of 41 Amethyst-throated Hummingbirds and 32 White-eared Hummingbirds mist-netted at Estación Científica Las Joyas in Manantlán Biosphere Reserve, Jalisco, Mexico (19°35'N, 104°16'W) between November 2004 and December 2005. To take the photographs, tails of individuals were held parallel to the camera lens (Figure 1A). Using these photographs, one of us (SG) measured the angle at the tip of R1 of each individual on a computer screen with MB Ruler software (Bader 2003–2015; Figure 1B). In order to minimize measurement error as well as to account for asymmetries between left and right R1, each feather was measured twice. Arithmetic mean of the two measurements was calculated and subsequently used in analyses. Age of each individual was determined by the combination of two criteria: extent of bill striations (Ortiz-Crespo 1972) and presence/absence of definitive plumage (*sensu* Howell & Webb 1995).

Sex was determined by the presence/absence of sexual ornaments (amethyst gorgets in male Amethyst-throated Hummingbirds; blue frontlet, upper blue-lower green gorgets plus red basal half of bill in male White-eared Hummingbirds), and their development (Howell & Webb 1995, Pyle 1997; Supplementary Online Material).

Hummingbirds have very protracted molts (Pyle 1997), especially so in tropical species (> 90% of all hummingbird species), which may not molt their juvenile remiges until 12 months after fledging (Stiles & Wolf 1974). For this reason, we grouped our birds in two age categories per sex: first-cycle and definitive-cycle (terminology based on Wolfe et al. 2010).

**Statistical analyses.** Pointedness was measured as angles (Figure 1B). Angular data fail to meet important properties of linear data, and requires the use of circular statistics (Fisher 1993). Our angular data fitted reasonably well a von Mises distribution (Watson's tests  $P > 0.10$ , except for the definitive female Amethyst Hummingbird subset, which was significantly different and, thus may lead to imprecise inference). The von Mises distribution allows to make inference from directional data (such as angles and vectors); it is easy to use and close to normal distribution (Fisher 1993). We used package circular (Agostinelli & Lund 2013) in R (R Core Team 2016) for testing between age differences (ANOVA of mean angle), computing bootstrapped 95% confidence intervals, and calculating discriminant ability. Discriminant power was evaluated as the probability of getting the maximum angle observed in first cycle birds on the distribution generated from the sample of definitive birds and *vice versa*. We used G\*Power (Faul et al. 2007) to calculate test power.



**Figure 1.** Analysis of rectrix morphology as age criterion for two Neotropical hummingbirds. Data were gathered at Estación Científica Las Joyas in Manantlán Biosphere Reserve, Jalisco, Mexico in 2005. A) Position of tail as photographed in the field (White-eared Hummingbird *Hylocharis leucotis*, captured on 4 October; photo by Santi Guallar); B) Measurement of angle at the tip of R1; C) Variation of R1 shape in the Amethyst-throated Hummingbird (*Lampornis amethystinus*); and D) variation of R1 shape in the White-eared Hummingbird. Rectrices are ordered from more pointed to more rounded. m = minimum, md = median, M = maximum, F = first cycle and D = definitive cycle.

## RESULTS

First-cycle Amethyst-throated Hummingbirds and White-eared Hummingbirds have more pointed R1 than definitive cycle individuals (Table 1). Sex differences are minor although males show slightly more rounded R1 (Table 1). Age differences were highly significant even after sequential Bonferroni correction (range of values for circular ANOVAs:  $19.51 < F < 46.47$ ,  $3 \times 10^{-6} < P < 0.003$ ). These differences were not explained by sex (range of values for circular ANOVAs:  $0.92 < F < 5.87$ ,  $P > 0.109$ ). Test power for differences of age within sex was very high ( $> 0.99$  in both species) due to very large effect sizes. Test power for within-age differences per sex was very low for the Amethyst-throated Hummingbird (0.07, 0.13) and

very high for the White-eared Hummingbird (0.88, 0.89). Discriminant ability of R1 for the sample of the Amethyst-throated Hummingbird was 75.6% for first-cycle birds and 80.9% for definitive birds. Discriminant ability for our sample of the White-eared Hummingbird was 98.9% for first-cycle birds and 98.2% for definitive birds.

## DISCUSSION

Central rectrix (R1) shape is a useful criterion for aging Amethyst-throated and White-eared Hummingbirds. However, our sample does not contain intermediate values among age classes, which might be a consequence of the small sample sizes. For this reason, the use of rectrix shape should be applied

**Table 1.** Pointedness of the central rectrix (R1) in Amethyst-throated Hummingbird (*Lampornis amethystinus*) and White-eared Hummingbird (*Hylocharis leucotis*). Data were gathered at Estación Científica Las Joyas in Manantlán Biosphere Reserve, Jalisco, Mexico in 2005. Estimated mean angle ( $\mu$ ) and concentration parameter ( $\kappa$ ) with their respective bootstrapped 95% confidence intervals (within parenthesis) per age-sex classes. Greater angles indicate more rounded tips. The concentration parameter is a reciprocal measure of dispersion ( $1/\kappa$  is analogous to  $\sigma^2$ ). Low sample size (n) of first-cycle female White-eared Hummingbirds precluded reasonable  $\kappa$  estimates. The units used are sexagesimal degrees.

Species	Parameter	First cycle		Definitive cycle	
		Females	Males	Females	Males
Amethyst-throated Hummingbird	$\mu$ (°)	91.2 (86.6–95.2)	94.2 (86.3–101.9)	126.0 (117.3–134.6)	128.6 (116.3–141.8)
	$\kappa$ (°)	50.4 (28.9–127.9)	50.4 (28.9–127.9)	13.7 (10.2–21.2)	15.6 (8.6–56.6)
	N	13	11	12	5
White-eared Hummingbird	$\mu$ (°)	113.2 (110.3–116.0)	106.6 (101.7–111.5)	138.6 (134.4–142.8)	143.7 (137.4–149.2)
	$\kappa$ (°)		40.2 (22.7–111.8)	63.7 (42.1–111.6)	63.7 (41.2–150.4)
	N	4	12	11	5

with caution, especially to the Amethyst-throated Hummingbird because of potential overlap between age classes.

Previous studies on the accuracy of rectrix shape as aging technique showed its adequacy to correctly age several passerines species. For example, Balph (1977) found that 15% of House Finches (*Haemorrhous mexicanus*) were misclassified, Collier & Wallace (1989) found about 5% of misclassified individuals among four species of thrushes, and Morris & Bradley (2000) found between 2% and 13% in four thrushes and 19 parulids. These studies mention wear in definitive cycle birds and rectrix loss and subsequent replacement in first cycle individuals as factors that partially explain misclassification. However, intermediate phenotypes apparently are responsible for the largest percentage of misclassifications. In this study, we did not observe noticeable rectrix wear, and rectrix replacement was readily detected by a contrast with adjacent rectrices (see two examples in the Supplementary Online Material).

Overall, in the current case the use of R1 shape meets three crucial properties of aging techniques: (1) High discriminant ability. It is optimal in the White-eared Hummingbird and high in the Amethyst-throated Hummingbird, although it does not reach an optimal level, which can partly be a consequence of the poor fit (see Statistical analyses; Table 1). (2) Wide temporal applicability. It can be applied during a period that spans eight (White-eared Hummingbird) to 12 months (Amethyst-throated Hummingbird) before the onset of the first prebasic molt. (3) Ease of use with minimum experience. Pointed vs. rounded R1 within a species can be rapidly learned and used in the field or in museums after comparing a few individuals with photographs or plates (e.g., Figures 1C–1D).

This study has two drawbacks. First, it is based on small samples sizes; however, lack of intermediate

individuals suggests its suitability as aging guide. Second, the information comes from a single population for both species, and morphometrics frequently vary among populations (e.g., Navarro et al. 2009, Guallar et al. 2010). To our knowledge, there are no accounts of drastic changes in rectrix shape among populations of resident bird species. However, this fact should not restrict the applicability of this technique at the species level: the important message is that juvenile rectrices are more pointed and definitive ones are more rounded, regardless of the absolute values. In any case, rectrix shape should be calibrated before application to a new population, by checking if it matches the expected between-age differences in R1 pointedness despite likely shifts in actual values (Tellería & Carbonell 1999, Waugh et al. 1999), or allometric effects (Tellería et al. 2013). Regardless of the actual biological relevance of the differences in R1 shape (Tellería & Carbonell 1999), studies on Neotropical hummingbirds will undoubtedly benefit from reliable species-specific aging criteria.

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