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RESEARCH ARTICLE

Feather growth rate increases with latitude in four species of widespread resident Neotropical birds

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ABSTRACT

The pace of life history events varies with latitude in many taxa. In birds, especially, life history events tend to be protracted in the tropics. This pattern is likely the result of reduced seasonality in resources and changes in trade-offs associated with risk of mortality. In general, animals invest more in reproduction per attempt and less in adult survival at higher latitudes. Feather growth is a major investment that birds make in their own survival, but geographic patterns of feather growth have received very little study. Evidence from separate studies of molt timing in individual species suggests that high-latitude species complete molt faster than tropical birds. Within species, feathers that are grown more quickly tend to show lower structural integrity than feathers grown more slowly, but seasonality of resources may place temporal constraints on the pace of feather growth. I hypothesized that increased seasonality of resources or decreased investment in adult survival in relation to reproduction would result in an increase in feather growth rate with latitude within species of birds. I tested this hypothesis and alternatives using ptilochronology methods to measure the growth rates of rectrices from museum specimens of 4 species of broadly distributed, resident Neotropical birds across their ranges. I compared these feather growth rates to latitude, climatic suitability, bioclimatic variables, sex, and body mass between and among species. I found that feather growth rate consistently increased with latitude in all 4 species. My results confirmed previous findings that feather growth rate increases with mass in a nonlinear fashion among species; but I found no consistent relationship between body mass and feather growth rate within species. I discuss these results in the context of life history theory and propose 3 potential mechanistic explanations for the relationship between feather growth rate and latitude within species, as (1) a programmed response to increasingly seasonal resources, (2) a decreased investment in adult survival, or (3) fixed to some other factor that may vary with latitude, such as basal metabolic rate.

Keywords: latitudinal gradients, life history, molt, Neotropical birds, ptilochronology

La tasa de crecimiento de las plumas aumenta con la latitud en cuatro especies de aves residentes neotropicales ampliamente distribuidas

RESUMEN

El ritmo de los eventos de la historia de vida varía con la latitud en muchos taxa. En las aves en particular, los eventos de la historia de vida tienden a prolongarse en los trópicos. Este patrón es probablemente el resultado de la disminución de la estacionalidad de los recursos y de los cambios en las soluciones de compromiso asociadas con el riesgo de mortalidad. En general, los animales invierten más en cada intento reproductivo y menos en la supervivencia del adulto a mayores latitudes. El crecimiento de las plumas es una inversión importante que hacen las aves para su propia supervivencia, pero los patrones geográficos de crecimiento de las plumas han recibido muy poca atención. La evidencia de diferentes estudios dedicados a la duración de la muda en especies individuales sugiere que las especies de altas latitudes completan la muda más rápido que las aves tropicales. Dentro de las especies, las plumas que crecen más rápido tienden a mostrar una menor integridad estructural que las plumas que crecen más lento, pero la estacionalidad de los recursos puede generar restricciones temporales en el ritmo de crecimiento de las plumas. En este estudio hipotetizo que una mayor estacionalidad de los recursos o una menor inversión relativa en la supervivencia del adulto respecto a la reproducción provocará un aumento en la tasa de crecimiento de las plumas con relación a la latitud dentro de las especies de aves. Evalué esta hipótesis y otras alternativas usando métodos de ptilocronología para medir las tasas de crecimiento de las plumas rectrices de las aves en especímenes de museo de cuatro especies de aves residentes neotropicales ampliamente distribuidas. Comparé, entre especies, estas tasas de crecimiento de las plumas con la latitud, la conveniencia climática, variables bioclimáticas, el sexo y la masa corporal. Encontré que la tasa de crecimiento de las plumas aumentó consistentemente con la latitud en las cuatro especies. Confirmé resultados anteriores que indican que la tasa de crecimiento de las plumas aumenta con la masa corporal de un modo no lineal entre especies; pero no encontré una relación consistente entre la masa corporal y la tasa de

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crecimiento de las plumas adentro de las especies. Argumento estos resultados en el contexto de la teoría de la historia de vida y propongo tres potenciales explicaciones mecanicistas para la relación entre la tasa de crecimiento de las plumas y la latitud adentro de una especie: (1) que es una respuesta programada al aumento en la estacionalidad de los recursos, (2) que es una disminución en la inversión en la supervivencia del adulto, o (3) que es algo vinculado a algún otro aspecto que puede variar con la latitud, como la tasa metabólica basal.

Palabras clave: aves neotropicales, gradientes latitudinales, historia de vida, muda, ptilocronología

INTRODUCTION

Life history in animals follows a pattern of increased pace at higher latitudes (Ricklefs and Wikelski 2002) and a slower pace in the tropics (Wiersma at al. 2007). This latitudinal gradient in the pace of life history is thought to result from trade-offs involved in seasonality of resources (Martin 1987, McNamara et al. 2008), predator avoidance (McKinnon et al. 2010), and longevity (Ricklefs 1980, Martin 2002). Latitudinal gradients in some aspects of life history, such as reproduction (Martin et al. 2006), migration (Ketterson and Nolan 1983, Alerstam et al. 2003), and hormonal concentrations (Silverin et al. 1997, Breuner et al. 2003), have been studied recently, especially in birds (Martin 2004).

Because investments in adult survival and in breeding attempts both demand an animal's time and energy, they act as antagonistic trade-offs in energetic decisions. Optimal strategies to approach this trade-off can vary with taxon and geography, and research into the pace of events related to adult survival can shed light on the dynamics of life history. A major, ubiquitous, discrete event that birds undergo for adult survival is an annual complete molt that replaces their feathers (Stresemann and Stresemann 1966). This molt is termed the prebasic molt (Humphrey and Parkes 1959). To date, there has been little research into latitudinal variation in the pace of prebasic molt.

Here, I ask whether birds show variation over their ranges in the pace of feather growth and investigate the effects of latitude and other plausible correlates on that variation. Feathers are important for flight, thermoregulation, crypsis, signaling, and other functions and must be replaced regularly to maintain function. Birds likely face a trade-off in feather growth rates, because faster rates in individual feathers appear to result in lower-quality feathers (de la Hera at al. 2009), but longer molting periods increase time spent with compromised feather utility. Some research has suggested that birds are able to adjust their molt intensity (i.e. the number of feathers molting at any one time) to change the timing of molt (Rohwer and Rohwer 2013). However, decreasing the time spent molting by molting more feathers at once results in larger gaps between feathers, which can compromise feather function through interruption of aerial and thermoregulatory dynamics. For example, significant gaps in a bird's wing during a high-intensity molt decrease flight ability (Guillemette et al. 2007). Birds that invest highly in reproduction in seasonal latitudes may thereby compromise their ability to molt feathers when beginning migration (Norris et al. 2004). In birds with a limited molting season, a slow molt may result in a molt that continues past the end of summer resource availability or overlaps with migration, which may be costly by compromising flight ability (Swaddle et al. 1997) or misappropriating internal energy reserves (Merilä 1997). By contrast, tropical birds, which live in less seasonal habitats, may not experience such constraints.

There is some evidence from previous research to support a latitudinal gradient in pace of molt. Among the species whose molt timing has been studied, the shortest molt period known occurs over a period of ~28 days in the High Arctic–breeding Snow Bunting (*Plectrophenax nivalis*; Green and Summers 1975). The longest molt known in passerines is in the tropical understory resident White-plumed Antbird (*Pithys albifrons*), which has been detected in molt throughout the year and whose individual molts may last >300 days (Johnson et al. 2012). The variation in overall timing of molt within species throughout their ranges has been the subject of a small number of studies in general (Holmes 1971, Williamson and Emison 1971, Mewaldt and King 1978, Hemborg et al. 2001), and there has been no research into latitudinal effects on feather growth rates.

There are 2 plausible mechanisms arising from latitudinal life history gradients that may affect feather growth rates within species. First, molt timing may be limited in areas with increased seasonality of resources. Second, a decreased investment in adult survival with higher latitudes may manifest as a faster production of lower-quality feathers. Because both of these potential mechanisms would result in increased rates of feather growth with latitude, I hypothesized that resident birds would show an increased pace of feather growth at higher latitudes.

Alternatively, feather growth rate may also be influenced by more proximate factors such as basal metabolic rate, body mass, or habitat quality. Basal metabolic rate varies geographically within animals, and evidence indicates that variation in basal metabolic rates within species is linked to latitude and ambient temperature in birds (Scholander et al. 1950, Daan et al. 1989). Feather growth rate within

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species may be influenced by body mass, as it is between species (Rohwer et al. 2009), through a link to either overall body size or energetic reserves. Habitat quality may affect feather growth rate through nutritive condition. Some research has suggested that nutritive stress may reduce feather growth rate (Grubb 1989; but see Murphy and King 1991). Birds in lower-quality habitats can show reduced feather growth rates on a local scale (Stratford and Stouffer 2001); therefore, birds inhabiting lower-quality portions of their species' ranges may potentially show reduced feather growth rates. These hypotheses fall into 2 main categories: (1) that feather growth rates within species throughout their ranges are influenced by the latitudinal gradient in the pace of life history events or (2) that variation in feather growth rates within a species is primarily a proximate response to local conditions.

METHODS

I used ptilochronology (Grubb 1989) to measure the pace of rectrix growth in widespread Neotropical birds in museum collections using specimens. To investigate the geographic patterns of feather growth rates within species, I examined 4 species that have large ranges that span a latitudinal gradient in both the Northern Hemisphere and the Southern Hemisphere, do not migrate, and are common in museum collections: Squirrel Cuckoo (*Piaya cayana*), Great Antshrike (*Taraba major*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), and Rufous-collared Sparrow (*Zonotrichia capensis*). I chose these species because they exhibit a broad latitudinal range in both hemispheres; are common species; are well represented throughout their ranges in museum collections; and are resident birds that do not undergo long-distance migrations, such that any individual can be reasonably assumed to have grown its feathers near where it was collected. (The southernmost subspecies of Rufous-collared Sparrow, *Z. c. australis*, is known to undergo long-distance movements and was omitted for this reason.) Most temperate-zone birds either undergo seasonal movements or have a comparatively narrow latitudinal range compared to the 4 study species.

Measurements of Feather Growth Rate

I measured feather growth rates using ptilochronology (Grubb 1989). Feathers show patterns of nonpigmented growth bars that result from slightly different growth during the day and night, and each pair of bars represents 24 hr of growth. I measured the rate of feather growth in rectrices of museum specimens by taking a photograph of the tail using a Canon EOS 7D digital camera with 100 mm Canon lens, while adjusting lighting either with a ring flash or external bulbs to maximize visibility of growth bars. I placed a metric ruler in each photograph next to the specimen, the same distance from the lens as the feathers. I then imported each photo into the image-processing software imageJ (Abràmoff et al. 2004) and calibrated a linear measuring device to millimeters using the ruler in the photo. I measured 5 sets of dark and light bars from approximately midway between the base and tip of each rectrix. I repeated this measurement 2 or 3 times to ensure accuracy and calibration. I also excluded any specimens with obvious fault bars because fault bars represent a severe nutritional deficit during feather growth (Grubb 1989), and their effects on surrounding growth bars are not known. Using this method, I measured specimens at the Louisiana State University Museum of Natural Science; National Museum of Natural History; Field Museum of Natural History; Western Foundation of Vertebrate Zoology; University of Florida; Natural History Museum of Los Angeles County; Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia; and Museu de Zoologia da Universidade de São Paulo. In these species, rectrices are grown during the prebasic molt. However, some Rufous-collared Sparrows may grow rectrices in prealternate molt (Pyle et al. 2015). In some alternate plumage feathers, a need to produce a bright or flashy plumage can result in feathers grown more quickly and at lower quality, and this may have affected my results, though rectrices in this species do not appear to serve as a separate sexual signal, and it is unclear whether there is a difference in the pace of growth in prealternate and prebasic molt in rectrices in this species.

Geolocation

For specimens without coordinate data, I used the program GEOlocate (Rios and Bart 2010) to find coordinates for localities by importing the locality from VertNet (Guralnick and Constable 2010) or directly from the specimen label. I then verified the localities individually by confirming the locality with the GEOlocate map portal and in Google maps. For each specimen, I verified each locality by checking the accuracy of the locality string with Google maps and the GEOlocate web app, and I corrected misplotted localities manually in cases where GEOlocate searched for the wrong part of the locality string or misinterpreted directions from towns or localities. Of the 1,723 specimens I measured, I geolocated 1,108 specimens (Figure 1). I removed 2 outliers of Rufous-collared Sparrow that were far above the distribution of feather growth rate for this species and thus likely resulted from some type of measurement or data-entry error. Some species (i.e. Great Antshrike) are easier to age than others (i.e. Squirrel Cuckoo) by molt limits and external characters; and many specimens lacked skull ossification, reproductive, or bursa data that would be useful for ageing. Therefore, I compared the feather growth rates of adult and first-cycle birds in specimens with age data of 3 species (Rufous-

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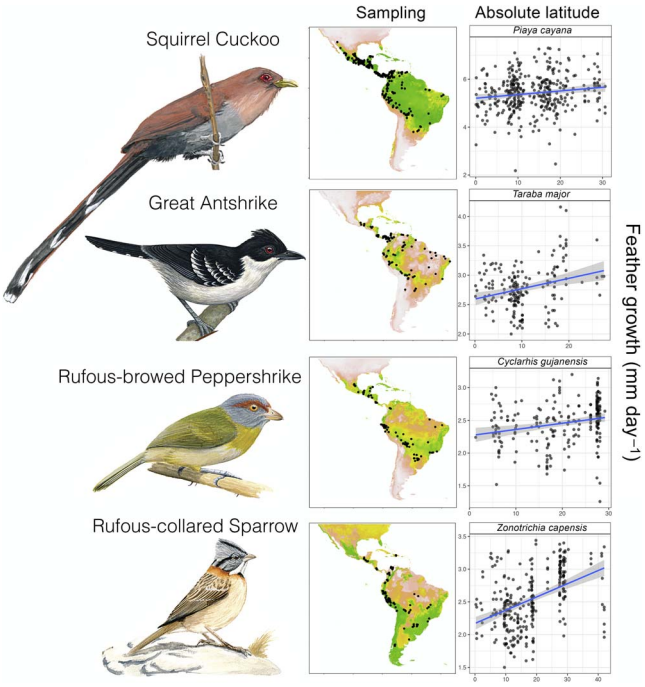

FIGURE 1. Sampling localities and comparison of feather growth rate to latitude in 1,108 specimens of 4 widespread, resident Neotropical bird species. Feather growth rates increased with latitude in all 4 species (Squirrel Cuckoo: $F_{1,360} = 7.794$, $P = 0.006$; Great Antshrike: $F_{1,170} = 15.37$, $P < 0.001$; Rufous-browed Peppershrike: $F_{1,212} = 17.88$, $P < 0.001$; Rufous-collared Sparrow: $F_{1,244} = 60.33$, $P < 0.001$). Black dots denote sampling localities; colors depict climatic suitability inferred from ecological niche modeling; *y*-axes are scaled to species because of the interspecific difference in range of feather growth rates.

browed Peppershrike, Great Antshrike, and Rufous-collared Sparrow), using Student's 2-sample *t*-test, which is robust to the small sample sizes in the number of juveniles sampled (de Winter 2013). I found no consistent difference in mean growth rate between age classes. Therefore, I included all age classes in this analysis to increase sample size, with the justification that including first-year birds should not skew the data. However, these birds undergo different molt strategies, and rectrices in young birds could represent formative (Rufous-browed Peppershrike) or juvenile (Rufous-collared Sparrow, and likely Great Antshrike) feathers (Johnson and Wolfe 2018). A larger study, with modern specimens with associated skull and gonad data, is needed to parse the ontogeny of feather growth rates in birds. I recorded each bird's sex where available from specimen tags and used Student's *t*-test to examine whether sex affects the rate of feather growth in these species.

I tested the effect of latitude on growth rates by constructing linear models of the rate of feather growth and the absolute value of latitude. I evaluated these models with the adjusted R^2, F, and P values of each models. I conducted all statistical analyses and data manipulation in R 3.3.1 (R Core Team 2016). Linear models assume a normal distribution of residuals from the model. I examined the applicability of this assumption to my data by generating Q-Q plots for each model, which compare observed to theoretical quantiles of the residuals of the data. I examined each plot to make sure that the assumption of normally distributed residuals was satisfied. I also constructed linear models to test alternative hypotheses for the rate of feather growth. I used label data from specimens for body mass and tested the relationship between body mass and feather growth rates by fitting a linear model to the log normalized body mass data and feather growth rates. I used this method to compare growth rate to body mass within species. Among species, I used linear models to compare feather growth rate to the body mass of the bird. I also constructed linear models to compare feather growth rates among species, by comparing feather growth rates to the mean mass for each species, including species as a fixed effect in each model. Resident tropical birds generally carry little subcutaneous fat, so I assumed that this would not be a confounding factor in body mass.

I tested the effects of climate suitability by constructing species distribution models for each of the focal species and comparing these models to feather growth rates in individual birds. I downloaded the full eBird dataset (Sullivan et al. 2009) and applied various data quality filters, thus excluding all checklists that covered >10 km, all invalidated records, and all observations from observers who had not recorded multiple observations of that species in the database, to exclude records from observers who might not be familiar with the species. I then plotted the remaining records and removed any with dubious locations. I downloaded the BioClim dataset (Hijmans et al. 2004) of 19 bioclimatic variables and constructed species distribution models using the filtered eBird localities and the BioClim variables in the package "dismo" (Hijmans et al. 2016), following the approach of Godsoe et al. (2009) with slight modifications for the different spatial scale of my dataset. Briefly, I plotted all presence points, and I obtained background points from 1,000 km circles around the presence points. I used both the presence points, background points, and 19 BioClim layers to model the distribution of each species using the Maxent algorithm via the R Java Maxent plugin in "dismo" (Hiimans et al. 2016). I then extracted climate suitability scores from the species distribution model at each point with a geolocated feather growth measurement and constructed linear models to evaluate their relationships. To evaluate whether feather growth rate responds to any individual variable, I constructed linear models between growth rate and each of the 19 bioclimatic variables and elevation (Table 1), as well as the elevation layer from the

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TABLE 1. Strength of correlations of bioclimatic variables and elevation with feather growth rate in 4 Neotropical bird species. Five variables, all related to temperature seasonality, predicted feather growth rates across all 4 study species. Asterisks indicate significant *P* values; rows in bold indicate variables where 3 or 4 species show significant *P* values.

	Squirrel Cuckoo		Great Antshrike		Rufous-browed Peppershrike		Rufous-collared Sparrow	
Variable	*P*	Adj. R^2	*P*	Adj. R^2	*P*	Adj. R^2	*P*	Adj. R^2
Annual mean temperature	0.121	0.007	0.337	0.005	0.648	0.006	<0.001*	0.124
Mean diurnal range	0.152	0.005	0.007*	0.041	0.952	0.0002	<0.016*	0.023
Isothermality	**0.006***	**0.021**	**<0.01***	**0.082**	**<0.001***	**0.058**	**<0.001***	**0.271**
Temperature seasonality	**0.017***	**0.015**	**<0.01***	**0.090**	**<0.001***	**0.076**	**<0.001***	**0.194**
Max temperature of warmest month	0.813	<0.001	0.289	0.006	0.108	0.003	<0.001*	0.145
Min temperature of coldest month	**0.027***	**0.017**	**0.017***	**0.033**	**0.367**	**0.003**	**<0.024***	**0.024**
Temperature annual range	**0.015***	**0.017**	**<0.001***	**0.084**	**<0.001***	**0.066**	**<0.001***	**0.116**
Mean temperature of wettest quarter	0.711	<0.001	0.185	0.01	0.84	<0.001	<0.001*	0.089
Mean temperature of driest quarter	**0.057**	**0.01**	**0.003***	**0.048**	**0.006***	**0.034**	**<0.001***	**0.039**
Mean temperature of warmest quarter	0.922	<0.001	0.674	0.112	0.011	0.003	<0.001*	0.213
Mean temperature of coldest quarter	**0.032***	**0.013**	**0.01***	**0.037**	**0.007***	**0.034**	**<0.006***	**0.03**
Annual precipitation	0.412	0.002	<0.001*	0.126	0.969	<0.001	0.172	0.008
Precipitation of wettest month	0.561	0.001	<0.001*	0.13	0.081	0.014	0.846	<0.001
Precipitation of driest month	0.626	<0.001	0.025*	0.029	0.003*	0.040	<0.001*	0.068
Precipitation seasonality	0.381	0.002	0.091	0.016	<0.001*	0.057	<0.001*	0.172
Precipitation of wettest quarter	0.462	0.002	<0.001*	0.120	0.01*	0.013	0.968	<0.001
Precipitation of driest quarter	0.597	<0.001	0.062	0.020	0.003*	0.040	<0.001*	0.058
Precipitation of warmest quarter	0.222	0.004	0.184	0.010	0.458	0.003	0.701	<0.001
Precipitation of coldest quarter	0.642	<0.001	0.003*	0.049	0.088	0.013	0.001*	<0.001
Elevation	0.486	−0.001	0.14	0.007	0.085	0.009	<0.001*	0.262

same dataset. I log transformed elevation and bioclimatic data and used a Box-Cox transformation to account for zero values in the dataset when they were present. I then examined histograms of the log transformed data and Q-Q plots of the residuals of the regressions to ensure that the data were approximately normally distributed after log transformation.

RESULTS

There were no consistent age-related effects between individuals in the 3 species with age data, although one species, Rufous-collared Sparrow, showed a decrease in growth rates in first-cycle birds (Great Antshrike: $t = -0.61$, df = 3.37, $P = 0.58$; Rufous-browed Peppershrike: $t = -0.78$, df = 7.65, $P = 0.46$; Rufous-collared Sparrow: $t = 2.56$, df = 70.78, $P = 0.012$). There were no differences between feather growth rates by sex in any of the species (Squirrel Cuckoo: $t = -0.54$, df = 167.64, $P = 0.59$; Great Antshrike: $t = -0.68$, df = 80.32, $P = 0.50$; Rufous-browed Peppershrike: $t = 0.38$, df = 169.11, $P = 0.71$; Rufous-collared Sparrow: $t = -1.57$, df = 202.8, $P = 0.12$).

Body mass and feather growth were not significantly related in regression analyses in 3 species (Squirrel Cuckoo: $F_{1,50} = 0.24$, $P = 0.63$; Rufous-browed Peppershrike: $F_{1,88} = 0.62$, $P = 0.62$; Rufous-collared Sparrow: $F_{1,107} = 0.06$, $P = 0.81$; Figure 2). Body mass was significantly negatively correlated with feather growth rate in Great Antshrike ($F_{1,45} = 68.15$, $P < 0.001$). To compare body mass and feather growth between species, I compared the feather growth rate of all individuals measured to the mean body mass by species, and then log transformed feather growth rate and body mass to account for the nonlinear relationship between these 2 variables. I log transformed both variables and conducted a linear model test and found that feather growth rate was highly correlated with mean body mass in all 4 species (adj. $R^2 = 0.85$, $F_{1,698} = 3{,}863$, $P < 0\ .001$; Figure 3).

I found a significant positive relationship between feather growth rate and latitude in all 4 species (Figure 1). The predictive power of latitude was low, but the probability of rejecting a null relationship was high (Squirrel Cuckoo: $F_{1,360} = 7.794$, $P = 0.006$; Great Antshrike: $F_{1,170} = 15.37$, $P < 0.001$; Rufous-browed Peppershrike: $F_{1,212} = 17.88$, $P < 0.001$; Rufous-collared Sparrow: $F_{1,244} = 60.33$, $P < 0.001$). This means that although latitude is likely not a main driver of variation in feather growth rates, the range of feather growth rates within a species does shift with latitude, and this shift is consistent and replicated across species. However, much variation is seen in individual sites, and well-sampled sites exhibited large amounts of the variance of the whole dataset (i.e. Corrientes, Argentina: Rufous-browed Peppershrike, SD = 0.288, $n = 66$ vs. full Rufous-browed

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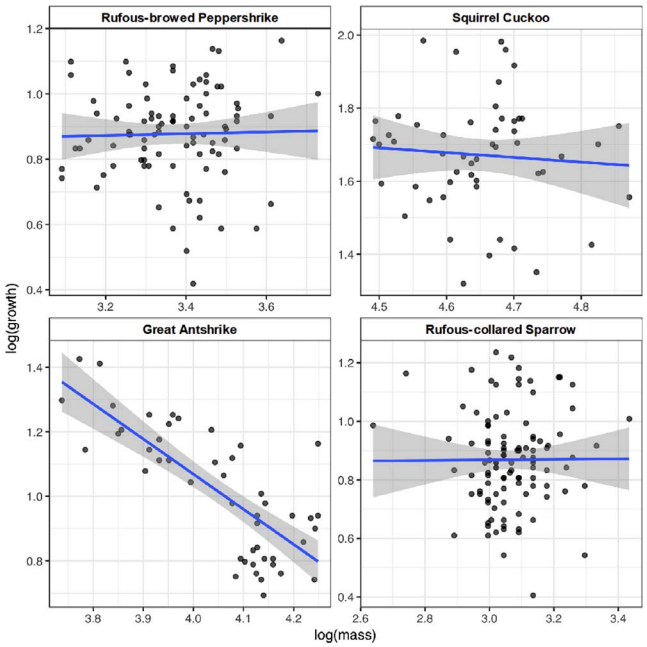

FIGURE 2. Feather growth rate vs. mass in rectrices of museum specimens of 4 Neotropical bird species. Mass measurements are from specimen data tags. No species shows a relationship between body mass and feather growth rate, except for an unexpected negative relationship in Great Antshrike. This pattern is the opposite of what might be predicted by the relationship between body mass and feather growth among species, and further research is needed to elucidate what, if any, mechanisms may have caused this relationship.

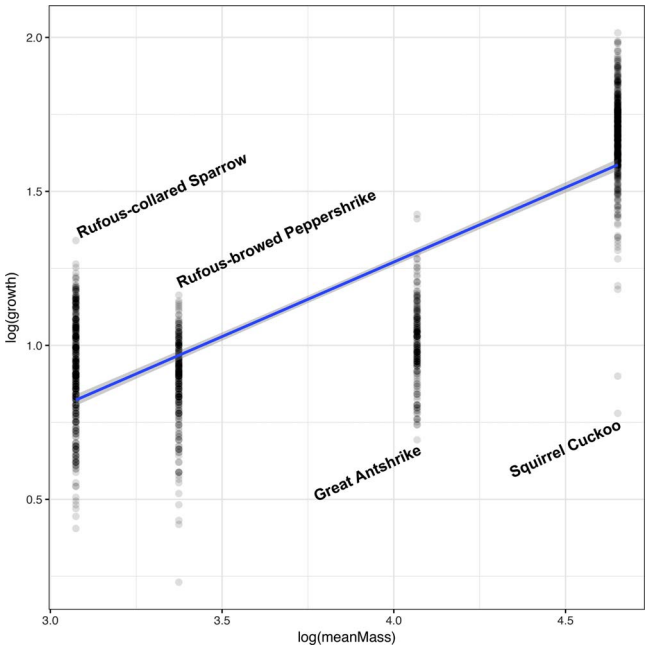

FIGURE 3. Relationship between mean body mass and individual feather growth rate in 4 Neotropical bird species. When log corrected for allometry and including species as a fixed effect, body mass strongly predicts feather growth rates among species (adj. $R^2 = 0.85$, $P < 0.001$).

Peppershrike dataset, SD = 0.33, n = 234; Corrientes, Argentina: Rufous-collared Sparrow, SD = 0.303, $n = 75$ vs. full Rufous-collared Sparrow dataset, SD = 0.429, $n = 348$), and this high within-site variance accounts, at least in part, for the weak geographic correlation coefficients. Nonetheless, a pattern of increased feather growth rate with latitude emerges across all 4 species.

I tested alternative hypotheses concerning plasticity in feather growth rates from environmental conditions in the focal species by comparing feather growth rates to climatic suitability, elevation, and 19 bioclimatic variables. I estimated climate suitability using species distribution modeling as a proxy. When I tested whether birds in sites with lower climate suitability showed reduced feather growth rate, I found no evidence to reject a null model of no relationship between feather growth rate and climatic suitability in 2 species (Squirrel Cuckoo: $F_{1,359} = 0.722$, $P = 0.40$; Great Antshrike: $F_{1,170} = 0.097$, $P = 0.71$), although the other 2 species showed a weak negative relationship between climate suitability and growth rate (Rufous-browed Peppershrike: adj. $R^2 = 0.015$, $F_{1,212} = 4.29$, $P = 0.04$; Rufous-collared Sparrow: adj. $R^2 = 0.11$, $F_{1,244} = 28.47$, $P < 0.001$), which may have resulted from clustering of growth data on the high end of climate suitability, where more individuals may have been sampled.

I found that 5 of the 19 bioclimatic variables showed weak but significant correlations with feather growth rates across all 4 species (Table 1): isothermality, temperature seasonality, minimum temperature of the coldest month, temperature annual range, and mean temperature of the coldest quarter, all variables associated with seasonality and temperature in some way. Precipitation in the driest month and precipitation in the driest quarter showed significant or nearly significant relationships in all species. The significant variables all involve seasonality of temperature, which could be evidence that increased seasonality drives feather growth rates across latitudes. Finally, Rufous-collared Sparrow (adj. $R^2 = 0.26$, $F_{1,244} = 87.77$, $P < 0.001$) showed a pattern of declining feather growth rates with elevation, and the other species did not show a significant relationship between elevation and feather growth rate (Rufous-browed Peppershrike: adj. $R^2 = 0.009$, $F_{1,210} = 2.99$, $P = 0.008$; Squirrel Cuckoo: $F_{1,339} = 0.53$, $P = 0.47$; Great Antshrike: adj. $R^2 = 0\ .014$, $F_{1,158} = 2.20$, $P = 0.14$).

DISCUSSION

Feather growth rate increased with latitude in all 4 study species. Although the correlations between latitude and

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feather growth rate are weak, the relationships are significant and replicated in each species. This repeated pattern appears to be in agreement with life history theory. If the pace of feather growth is an investment in adult survival, birds may decrease investment in feather quality by growing lower-quality feathers in order to free up time and resources for reproduction. I interpret this as evidence that feather growth rate follows the general latitudinal gradient, seen in other life history traits, of a slower pace of life toward the tropics (Wikelski et al. 2003, Wiersma et al. 2007). Furthermore, I found that feather growth rate correlates with 5 bioclimatic variables that are all involved in seasonality of temperature, and may be related to 2 other variables related to seasonality of temperature. This may indicate a link between seasonality of resources and feather growth rates throughout the ranges of birds. At any given latitude, there is variation in feather growth rate within species (Figure 1). This within-site variation is likely in response to various factors and may be a proximate response to food availability or external conditions, as has been shown in various laboratory experiments (Grubb 1989).

I found no association between predicted climatic suitability and feather growth. I interpret this result, combined with the within-site variation in feather growth rate, as evidence that large-scale climatic suitability is not a main driver of feather growth rates in birds. Birds may respond to proximate stressors with a decrease in feather growth rate, but this does not seem to manifest on a distribution-wide scale. It may be the case that local adaptation is strong enough that individual populations are well suited to their climatic conditions, or at least strong enough as to obscure an overall relationship between climate suitability and feather growth rate. However, species distribution models, as I constructed them, are at best a crude proxy for climatic suitability for any individual bird at any given site, and this result should be considered a first pass at the potential interaction between climate and feather growth over a species' range. Much more research is needed, in general, into the biogeography of stress response and the physiological consequences of local adaptation.

My body mass data confirmed the finding of Rohwer et al. (2009) that body mass is tightly linked to feather growth among species. That study used only a few individuals for each species; by including larger sample sizes, I found that this pattern is consistent across 4 species, across their ranges and across the range of phenotypic variation inherent within each species. I also found no relationship between body mass and feather growth rate within 3 species, which I interpret as evidence that body mass does not drive variation in feather growth rate within species, as it does between species. However, my study was designed to increase sample sizes by including as many specimens as possible and, thus, most specimens examined did not have associated body fat data. Therefore, an underlying pattern linking feather growth rate to body size or energetic reserves within species may exist, and a future study concentrating on modern specimens and including more morphological data could address this question. The strong negative relationship between body mass and feather growth rate in the Great Antshrike was surprising. The Great Antshrike shows a high amount of interspecific morphological diversity and may represent multiple cryptic species. However, if these populations represented cryptic species, one would expect an increase in feather growth rates with mass, as is the case among species. There seemed to be no bioclimatic variables that uniquely influenced feather growth rate in Great Antshrikes (Table 1). Further study with more species will be necessary to figure out which, if any, other species show this pattern and what similarities they may have that would explain the pattern. The relationship between body mass and feather growth rate within and among species is similar to the way that basal metabolic rate interacts with body mass in birds (Bennettand and Harvey 1987, Daan at al. 1989), in that it shows a strong relationship among species, but little or none within species. A plausible mechanistic explanation, therefore, for the latitudinal gradient in feather growth rates may be that birds at higher latitudes have higher basal metabolic rates, and this influences the rate of feather growth. This is consistent with evidence for relationships between temperature and precipitation and basal metabolic rates in birds (Scholander et al. 1950, Williams and Tieleman 2000, White et al. 2007) and mammals (Lovegrove 2003). Lindström et al. (1993) found evidence that basal metabolic rate is proportional to the cost of feather production within 2 bird species. Feather growth rates were weakly but significantly correlated to 5 temperature variables, but all of these variables also measured seasonality in some respect, so it is difficult to disentangle the relative influences of ambient temperature during the molting period and seasonality of resources on feather growth rates on the basis of these results. However, high elevation results in low temperatures even at tropical latitudes but did not increase feather growth rate. In fact, the 2 species that showed a response to elevation, Rufous-browed Peppershrike and Rufous-collared Sparrow, showed a marked decrease in feather growth rate with increased elevation.

I found that birds at higher latitudes tended to grow their feathers at a faster rate than conspecifics closer to the equator. This effect is likely to be stronger in birds outside the tropics, as seasonality becomes increasingly significant. This pattern agrees with life history theory, which posits that the pace of life history traits tends to accelerate in seasonal environments, and that investment in adult survival in relation to reproductive attempts decreases

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with increasing latitude. This pattern is likely due to either (1) a decreased investment in feather quality, as a reflection of decreased investment in adult survival in relation to reproduction; or (2) a compressed season available for feather growth. Alternatively, this pattern could be (3) a function of a link between basal metabolic rate and feather growth rate. Further work on individual variation in basal metabolic rate and feather growth rate between temperate and tropical sites is needed to understand whether the latitudinal gradient in feather growth rates is the product of an adaptive response to seasonality, a byproduct of increased basal metabolic rate, or a combination of the two.

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Ethics statement: The author followed all standard and required practices for examining specimens in natural history museums.

Data deposits: Data are deposited at https://github.com/enicurus/ptilochronology/blob/master/Feathergrowthdatabase.csv

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