HOW DO BIRDS ADJUST THE TIME REQUIRED TO REPLACE THEIR FLIGHT FEATHERS?

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Abstract.—Regular replacement of flight feathers is one of the most time-consuming activities in the annual cycle of flying birds. In principle, birds can decrease the time required to renew feathers by increasing the rate at which individual feathers grow and by growing more feathers simultaneously. Using 52 comparisons of 43 species from 26 families of birds that maintain the ability to fly while molting, we show that the average number of primary feathers growing simultaneously explains 60.0% of the variation in mass-corrected molt duration, whereas feather growth rate explains only 4.4% of the variation in mass-corrected molt duration. The trend is even stronger when species that grow all their primaries simultaneously are included in the analysis. We suggest that the rate at which feather tissue is produced cannot increase without compromising feather quality because the size of the feather follicle constrains the speed at which feathers can be generated. Thus, birds that must molt rapidly to meet time constraints in their life cycle may be forced to reduce the time spent molting mostly by growing more feathers simultaneously. *Received 6 March 2013, accepted 11 July 2013.*

Key words: feather growth rate, feather quality, molt intensity, ptilochronology.

¿Cómo Ajustan las Aves el Tiempo Requerido para Reemplazar sus Plumas de Vuelo?

Resumen.—El reemplazo regular de las plumas del vuelo es una de las actividades que más tiempo consumen en el ciclo anual de las aves voladoras. En principio, las aves pueden disminuir el tiempo requerido para renovar las plumas incrementando la tasa a la que crecen las plumas individuales y produciendo más plumas simultáneamente. Usando 52 comparaciones en 43 especies de 26 familias de aves que mantienen la habilidad de volar durante la muda, demostramos que el número promedio de plumas primarias que crecen simultáneamente explica el 60.0% de la variación en la duración de la muda (corregida por masa), mientras que el crecimiento de las plumas solo explica el 4.4% de la variación en la duración de la muda (corregida por masa). La tendencia es aún más fuerte cuando se incluyen en el análisis especies que mudan todas sus primarias simultáneamente. Sugerimos que la tasa a la que se produce el tejido de las plumas no se puede incrementar sin comprometer la calidad de éstas debido a que el tamaño del folículo de las plumas restringe la velocidad a la que se pueden generar. Por lo tanto, las aves que mudan rápidamente para cumplir con restricciones de tiempo en su ciclo de vida podrían verse forzadas a reducir el tiempo que pasan mudando mediante el crecimiento simultáneo de más plumas.

The feathers of birds are nonliving keratinaceous tissue of extraordinary strength and lightness. Despite the remarkable qualities of keratin, feathers wear out and must be replaced regularly to meet the demands of thermoregulation and flight. For birds that maintain the ability to fly while molting, the duration of primary molt scales with mass (M) as $M^{0.145}$ (S. Rohwer et al. 2009). This relatively small allometric coefficient between molt duration and body size suggests that the replacement of the flight feathers is one of the most time-demanding activities in the annual cycle of large birds, and sets up molt as an important time constraint in avian life-history studies.

Tradeoffs in the time and energy allocated to molt have immediate and long-lasting effects on individual fitness. During flight feather molt, birds face immediate challenges of impaired flight performance, increased susceptibility to predation, and increased energy demands of generating new feathers (Tucker 1991, Murphy and King 1992, Swaddle and Witter 1997). Tradeoffs in time and energy allocated to a single episode of molt can also have long-lasting effects on feather quality. In small birds, hurried molts can result in lower-quality feathers, increased thermoregulatory costs, reduced winter survival, and low reproductive success during the subsequent breeding season (Nilsson and Svensson 1996, Dawson et al. 2000, Serra et al. 2007). Moreover, in an albatross, worn flight feathers are associated with reduced reproductive success in the current breeding season and with a reduced probability of breeding

in the subsequent season (Rohwer et al. 2011). These links between feather quality and fitness suggest that feather quality may be the currency through which the time demands of molting are exposed to selection over the entire annual cycle.

The time required to replace the primary flight feathers (the long outer flight feathers that attach to the hand) is a good index of the time spent replacing the entire plumage for birds that maintain flight during the molt. How birds reduce the time spent replacing primaries has not been addressed rigorously. Several investigations consider the importance of growing more feathers simultaneously (e.g., Dawson 2004, Serra and Underhill 2006, V. G. Rohwer et al. 2009), but the relative contribution of flight feather growth rate and the number of flight feathers replaced simultaneously (molt intensity) to the time required to replace the flight feathers has not been addressed.

Because flight feather growth rate increases as an allometric constant with body (S. Rohwer et al. 2009) and feather size (de la Hera et al. 2012), within-species differences in flight feather growth rate might be assumed to have little effect on molt duration. However, the relationship merits investigation for several reasons. First, there is variation around the line of allometry relating feather growth rate to body mass or feather length, and some of this variation may be related to different life histories, rather than measurement error (S. Rohwer et al. 2009, de la Hera et al. 2012). Indeed, Willow Warblers (*Phylloscopus trochilus*), which molt twice a year, grow their primaries more slowly during their African winter molt than in their European postbreeding molt (de la Hera et al. 2011). Second, there is growing evidence that some groups of birds grow their feathers at different rates when the effects of body and feather size on growth rate are removed (de la Hera et al. 2012, Johnson et al. 2012, V. G. Rohwer and S Rohwer unpubl. data). Finally, flight feather growth rate has been related to molt duration in several recent studies (de la Hera et al. 2011, 2012; Echeverry-Galvis and Hau 2012). These points suggest that a rigorous assessment of the relative importance of feather growth rate and molt intensity to adjust the duration of molt would inform the role of feather production, quality, and wear in shaping avian life histories.

We assess the relative contribution of primary growth rate and primary molt intensity in explaining variation in the duration of primary replacement across a diversity of birds. Only a single study has evaluated the role of feather growth rate and molt intensity, and it showed no effect of feather growth rate on molt duration when molt intensity was included in the analysis (de la Hera et al. 2011). Remarkably, no comparative study has asked how feather growth rate and molt intensity reduce the duration of molt, probably because molt studies seldom report feather growth rates. To overcome this deficiency, we measured feather growth rates using growth bands (paired light–dark bands visible in feathers; Michener and Michener 1938, Grubb 1989) for a set of species for which we found data on molt duration and intensity. Using 52 comparisons of 43 species, spanning 26 families of birds that fly while molting, we show that birds reduce the time required to molt primarily by growing more feathers simultaneously.

Methods

We performed three different analyses using three independent data sets. Data collection and statistical methods specific to each analysis are presented in each section. For each analysis, we measured growth bands by placing a slip of paper under the feather of interest and marking sequential growth bands by puncturing the paper with a pin (Grubb 1989). When possible, we used ≥10 intervals to estimate the mean rate of feather growth; for some species, feathers were too short or bands too difficult to see to measure 10 intervals. We required a minimum of five consecutive growth bands from a feather in order for species to be used in our analyses.

Comparing measures of feather growth rates.—To validate the use of feather growth bands as estimates of daily feather growth, we compared direct measures of primary growth rate in 43 species; these measures come from published estimates of feather growth rates made by repeated measures of growing feathers on the same individual (see table 1 in S. Rohwer et al. 2009). These direct measures were compared with estimates of primary growth rate for 34 different species made by measuring growth bands in their primaries from museum specimens. Unfortunately, comparisons of direct and indirect measures of primary growth rate were not paired by species or individual because growth bands could not be seen in the primaries of many of the species for which the literature provided direct measures of feather growth rates or because those species were not available in the museum collections we used.

Because S. Rohwer et al. (2009) found no effect of phylogeny on feather growth rates in their analysis of 43 species, we did not control for phylogeny in the 34 species we used to estimate feather growth rates from measures of growth bands. There is also little reason to think that molt duration would be constrained by phylogeny because the duration of the primary molt is very different for the pre- and postbreeding molts of the Willow Warbler (Underhill et al. 1992) and the Black-chested Prinia (*Prinia flavicans*; Herremans 1999), and for migrant shorebirds, often of the same species, molting at different latitudes (see table 6 in Marks 1993). Thus, adding independent contrasts to this analysis would simply make the results less accessible. We used a diversity of bird species that encompassed the range of variation in body mass found in the 43 species analyzed by S. Rohwer et al. (2009). We tested for differences in feather growth rate as a result of direct and indirect measures for assessing primary growth rate using a general linear model. Feather growth rate was our dependent variable, and body size, method of measuring feather growth rate (direct and indirect), and a body size × method interaction were our independent variables. Body size and feather grow rate were log 10 transformed to normalize these data.

Factors affecting feather growth rates.—Growth bands are often difficult to see in the primaries, but they can easily be seen and measured in other feather groups of many species; thus, it was important for us to relate feather growth rate in other feather groups with those in the primaries so that growth band measures made from other feathers could be used to estimate primary growth rate.

To validate this approach, we assessed how feather group and feather size influence feather growth rates by measuring growth bands from four feather groups (primaries, rectrices, secondaries, and secondary coverts) on the same specimen from 28 adults of 27 species from 24 families of birds (Table S1 in online supplementary material; see Acknowledgments). We treated male and female Northern Jacanas (*Jacana spinosa*) separately because females are considerably larger than males. For each specimen, we measured growth bands from one rectrix, one primary, one secondary, and one secondary covert. Within feather groups, the

feather measured varied because we could not see growth bands in all feathers. For each feather for which growth bands were measured, we assessed feather size by measuring the length of the feather and the diameter of the feather shaft at the base of the feather. These size measures were strongly correlated with feather growth rate (least-squares linear regression of feather growth rate regressed on feather length: $r^2 = 0.72$, $P < 0.001$; feather growth rate regressed on diameter of feather shaft: $r^2 = 0.71$, $P < 0.001$) and with each other (diameter of feather shaft regressed on feather length: $r^2 = 0.92$); thus, we used only feather length as a measure of feather size in subsequent analyses (de la Hera et al. 2012). We did not measure feather mass because that would have been destructive of museum specimens.

We tested how feather group and feather size influence feather growth rates using a general linear model with feather growth rate as our dependent variable and feather group (primary, secondary, rectrix, or secondary covert), feather length, and a feather group * feather length interaction term as independent variables. For this analysis, both feather growth rate and feather length were log 10 transformed to normalize their distributions.

Comparing growth rate and molt intensity.—We first summarized studies from 12 species of birds that show intraspecific variation in the duration of their primary molt in either natural (e.g., geographic or seasonal) or experimental studies. We examined whether shorter molt durations within species are achieved by increasing feather growth rates or by replacing more feathers simultaneously using binomial sign tests; feather growth rates were not available for all 12 species.

Second, we used 52 comparisons from 43 species (in 26 families) to assess the relative contributions of feather growth rate and molt intensity to molt duration; some species included in our analysis had multiple measures of primary molt duration, intensity, and feather growth rate because of geographic variation, sex, or experimental manipulation; thus, the number of comparisons exceeds the number of species used in our analysis (for a summary of comparisons and species used, see Table S2 in online supplementary material; see Acknowledgments). We did not include in statistical analyses species that replace their primaries so simultaneously that they lose the ability to fly. (However, we included five species of simultaneous molters in Fig. 3 to illustrate cases of extreme molt intensity.) Data come from field studies and from a few experimental studies that manipulated molt speeds by varying light–dark cycles. For species with multiple estimates of molt duration and intensity due to seasonal, geographic, or population differences in timing of molt, we measured feather growth rates (using growth bands visible in the feathers) from museum specimens that corresponded to appropriate seasonal or geographic differences. Care was taken to measure growth bands in postjuvenile plumages, with age classes recognized by molt limits, comparisons with other specimens, and label notes on skull pneumatization and the presence or absence of a bursa.

Most published estimates of primary molt duration were calculated using either regression (Pimm 1976) or maximum likelihood (Underhill and Zucchini 1988) models. The regression model (Pimm 1976) has been criticized for overestimating molt durations because its residuals are not normally distributed along the regression line (Underhill and Zucchini 1988). However, the overestimates are trivial compared with the several-fold differences in molt duration found among the species included in our analyses (Rohwer and Broms 2012). A larger problem with regression and

likelihood estimates of molt duration is that both models assume a high degree of synchrony in the scheduling of molt among individuals, something that fails badly in species of the wet tropics that may molt year round (Rohwer and Wang 2010, Johnson et al. 2012). When molt is poorly synchronized, both models overestimate molt duration (Rohwer and Broms 2012, Rohwer 2013). For the two species with asynchronous molt included in this analysis, molt duration was calculated from the lengths, loss intervals, and growth rates of the primaries (Rohwer and Wang 2010, Rohwer 2013). We did not include the technique of estimating molt duration as a factor in this analysis because the application of regression and likelihood methods is structured geographically and molt duration has a strong geographic component.

When growth rate and intensity data were not published, we measured these variables using the following methods. We measured growth bands in the primaries if we could see them there. When growth bands could not be seen in the primaries, we measured them in the rectrices and converted them to estimates of primary growth rate using a regression that corrected for feather size and feather group (see below). When log 10 feather growth rate has been regressed on log 10 feather length for various groups of feathers, the general equation for converting growth rate measures of one feather group to another is $G_d = 10^{[(m_d \times L_d) - b_d] + G_p - [(m_p \times L_p) - b_p]}$, where G_d is the estimated feather growth rate of the desired feather or feather group (in our case the primaries), m_d is the regression coefficient (slope) of the desired feather group, L_d is the log 10 length of the feather or average lengths of the desired feather group, b_d is the intercept of the desired feather group, G_p is the log 10 growth rate of the predictor feather from a different group (in our case the rectrices), m_p is the regression coefficient of the predictor feather's group, L_p is the log 10 length of the predictor feather, and b_p is the intercept of the predictor feather's group (for m and b values for the primaries, secondaries, rectrices, and secondary coverts, see Table 1). This general equation controls for differences in growth rate due to feather size and group and assumes that deviations in growth rates of the predictor feather from the predictor feather's regression coefficient (Table 1) are species specific and also observed in the feather group for which growth rates are being estimated.

Our estimates of primary feather growth rate are averages from two adult males and two adult females to control for possible sex differences in feather growth rates (Grubb 1989). We used a minimum of five growth bands per individual; thus, our estimates of feather growth rates for species included in this analysis are the average of ≥ 20 growth bands per species, usually from two adult males and two adult females. For some species, we could not measure equal numbers of males and females, either because one

TABLE 1. Regression coefficients (± SE) and intercepts (± SE) calculated from our general linear model for the linear regressions of log 10 feather growth rate regressed on log 10 feather length for four feather groups (primaries, secondaries, rectrices, and secondary coverts) presented in Figure 2B.

Feather group	Coefficient (m)	Intercept (b)
Primaries	0.4681 ± 0.068	−0.3228 ± 0.139
Rectrices	0.5937 ± 0.055	−0.6640 ± 0.113
Secondaries	0.4597 ± 0.067	−0.2941 ± 0.132
Secondary coverts	0.5273 ± 0.054	−0.4799 ± 0.088

sex was not available in the collections we used or because growth bands were not visible in both sexes; these are noted in Table S2.

Our estimates of molt intensity are the average number of primaries growing simultaneously per wing between the second and the next-to-last functional primary. These data come from published studies or were calculated using methods described in Yuri and Rohwer (1997). Species included in this analysis replace their primaries sequentially, starting from innermost (P1) and proceeding to outermost (P9 or 10). As an example, in a molting bird in which P5 is the outermost growing primary, we counted P5 and all more proximal growing feathers as the measure of molt intensity for that individual. Similar values are then computed for each bird replacing primaries, eventually giving intensity values for all of the primaries. These values can then be converted to average numbers of growing feathers for each outermost growing primary, which are then averaged from P2 to the next to last functional primary to give the average molt intensity values used here. Average molt intensity was more appropriate to these analyses than peak molt intensity (V. G. Rohwer et al. 2009) because some species drop their inner primaries in rapid succession and their long outer primaries more slowly (Holmes 1966, Prater 1981). Peak molt intensities given in V. G. Rohwer et al. (2009) were recalculated as average molt intensities here.

To assess the relative contributions of primary growth rate and molt intensity to the duration of the primary molt, we used a general linear model (GLM) with duration as the dependent variable and body mass, feather growth rate, and primary molt intensity as independent variables. For this analysis, primary molt duration and body size were log 10 transformed to fit normal distributions, but primary growth rates and molt intensity were not transformed, because the raw data were normally distributed. We selected the best-fit model using forward model selection, whereby models started simple and became more complex. First we examined the contributions of body mass and feather growth rate to molt duration, and then we examined body mass and molt intensity on duration. Both growth rates and intensity were significant predictors when placed alone with body mass in a GLM model, so we combined all three variables into a single model. We then added all possible two-way interaction terms, but we removed these because no two-way interaction was significant. Finally we added and removed the three-way interaction, which also was not significant.

RESULTS

Comparing measures of feather growth rates.—We found no difference between feather growth rates estimated from repeated measures of growing primaries on live birds and growth bands measured from the primaries ($P = 0.79$; Table 2 and Fig. 1). Both measures of feather growth rate increased at similar rates with body size (GLM; method * body size, $P = 0.12$ [Table 2]; growth bands: $r^2 = 0.63$, $y = 0.13x + 0.35$, $n = 34$; repeated measures of growing feathers: $r^2 = 0.71$, $y = 0.17x + 0.24$, $n = 47$). The similarity between these two measures validates using growth bands to estimate feather growth rates. We had growth-rate measures from both growth bands and repeated measures of growing feathers for only a single species, the Siberian Crane (*Grus leucogeranus*), and each method yielded similar measures of feather growth rate (growth bands = 8.1 mm day^{-1}, repeated measures of growing feathers = 9.0 mm day^{-1}).

Factors affecting growth rates of feathers.—Both feather group ($F = 81.7$, df = 4 and 107, $P < 0.001$) and feather length ($F = 300.0$, df =

TABLE 2. Summary of a general linear model comparing two methods of measuring feather growth rate. Statistics compare direct (multiple measures of growing feathers on live birds) to indirect (growth bands visible in feathers) measures of feather growth rate; the nonsignificant interaction term between body mass and method of measuring feather growth rate suggests that growth bands are appropriate for assessing feather growth rate.

Variable	df	F	P
Body mass	1 and 73	163.77	<0.00001
Method of measurement	1 and 73	0.076	0.78
Body mass * method	1 and 73	2.48	0.12

4 and 107, $P < 0.001$) strongly affected feather growth rates (Fig. 2). The significant effect of feather group on feather growth rates shows that mean growth rates (intercepts) vary by feather group. However, feather group had no effect on the slopes relating feather growth rate to feather length (GLM; feather group * feather length interaction, $F = 1.1$, df = 7 and 104, $P = 0.37$; Fig. 2). Although feather groups have different mean growth rates, they scale with feather length at about equal rates. Thus, measures of feather growth rates made in different feather groups become comparable by correcting for feather size and by adding or subtracting a constant (when data are log 10 transformed), depending on which feather group was used to estimate growth rate. Although slopes between feather groups are not statistically different, we present feather-group-specific coefficients in Table 1, extracted from our GLM, for more accurate conversion between feather groups.

Comparing growth rate and molt intensity.—Table 3 summarizes feather growth rate, molt intensity, and molt duration data for 12 within-species comparisons that have different molt durations associated with experimental manipulations, geographic variation,
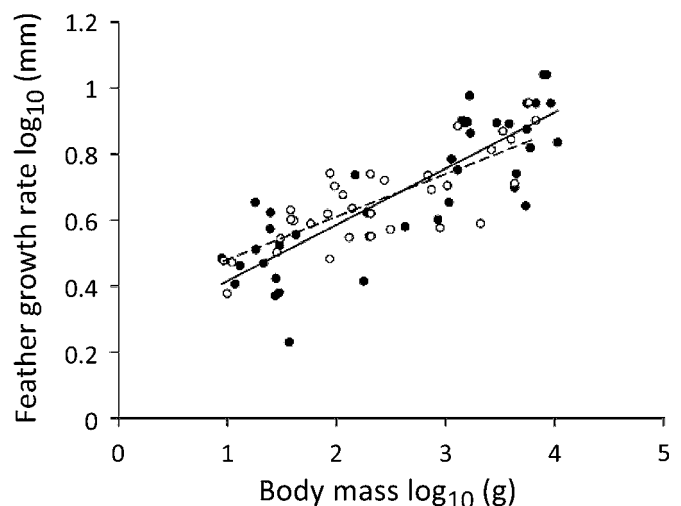

FIG. 1. Comparison between two measures of feather growth rates and body mass. Unfilled circles are estimates of primary feather growth rates measured from growth bands in museum specimens ($n = 34$). Filled circles are estimates of primary feather growth rates taken from repeated measures of growing primaries in live birds ($n = 47$). There is no difference in the slope of these growth rate measures or the intercepts (Table 2), which suggests that growth bands provide reliable estimates of feather growth rates.
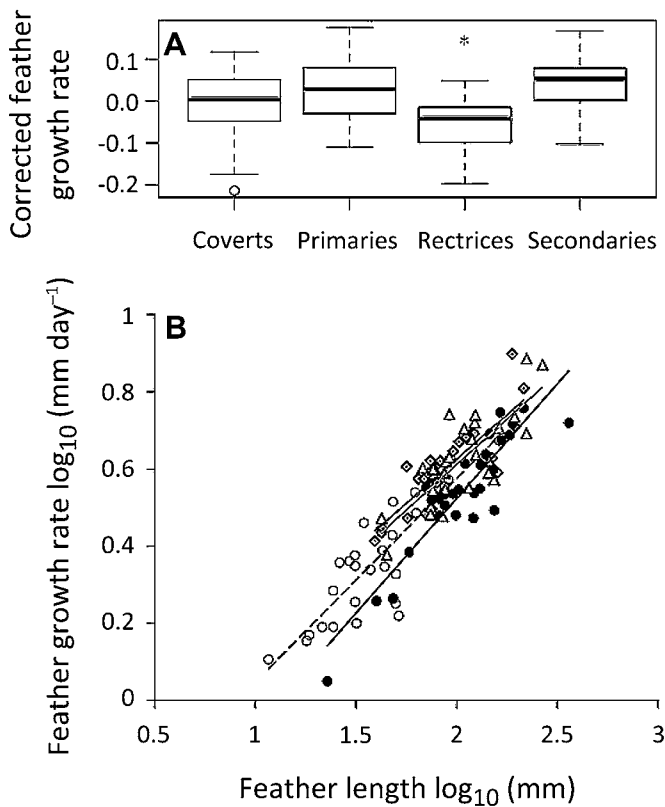
FIG. 2. Relationships between feather group, feather growth rates, and feather size. We measured four feather groups: primaries, rectrices, secondaries, and secondary coverts. Each group was measured on the same individual using 28 museum specimens from 27 species. (A) Corrected feather growth rate when feather size (measured as length) is controlled for; rectrices grow at slightly slower rates for a given feather size. (B) Relationship of feather growth rates (measured from growth bands) and feather length for the four feather groups. Starting from the topmost line, feather groups include the secondaries (gray diamonds, solid dark gray line), primaries (gray triangles, solid pale gray line), secondary coverts (unfilled circles, dashed line), and rectrices (filled circles, solid black line). The rate at which feather growth rate increases with feather length is not statistically different for each feather group. These plots show that growth bands are comparable between feather groups when corrected for feather size and group.

or seasonal variation in molt duration. Eleven of these 12 species reduced their molt durations by growing more feathers simultaneously (binomial sign-test, $P = 0.006$). Eight of these 12 species had data for feather growth rates, and of these eight species, four reduced their molt durations by increasing feather growth rates (binomial sign-test, $P = 1.0$). This within-species comparison suggests that the number of feathers grown simultaneously is a labile trait, and that shorter molt durations are achieved by growing more feathers at once.

For our 52 comparisons involving 43 species, the duration of the primary molt was best explained by body mass, molt intensity, and feather growth rate. Molt duration increased strongly with mass ($P < 0.001$; Table 4) and decreased strongly with molt intensity ($P < 0.001$; Table 4 and Fig. 3). By contrast, feather growth rate was weakly associated with molt duration ($P = 0.018$; Table 4

and Fig. 3), such that as feather growth rate increased, duration decreased. No interaction term was significant. Excluding the effect of body mass, primary molt intensity accounted for 60.0% of the variance in molt duration whereas primary feather growth rate accounted for 4.4%, a 13.6-fold difference in explanatory power (Table 5). This large comparative data set shows that rapid replacement of all the primaries is predominantly accomplished by growing more feathers simultaneously.

DISCUSSION

Our results allow us to make three main points. First, growth bands measured from the primary feathers provide estimates of the daily rate of feather growth that are comparable to the values obtained from repeated measures of growing feathers (Fig. 1). Of course, this applies only to species that lay down a single pair of light–dark growth bands in a 24-h period, and some species and age classes do not meet this assumption (Langston and Rohwer 1996, Kern and Cowie 2002). Second, feather growth rates are strongly influenced by feather size and also by feather group. However, the rate at which feathers grow (as measured from growth bands) increases with feather size at similar rates among the four groups of feathers we measured (primaries, secondaries, rectrices, and secondary coverts); thus, measures of feather growth rates made from one feather group can be used to estimate the growth rate for feathers of another group as long as feather size and group are controlled for (Table 1 and Fig. 2). Third, growing more feathers simultaneously predominates as the mechanism by which birds reduce the duration of primary replacement (Table 3 and Fig. 3). The relative importance of feather growth rate in determining molt duration may increase as more data on wet tropical residents becomes available because these species generally have long molt durations and slightly slower feather growth rates (Rohwer and Wang 2010, Johnson et al. 2012).

Feather growth rates and feather quality.—Accelerated flight feather molts typically result in shorter feathers, increased wear, and reduced structural integrity of the flight feathers (Nilsson and Svensson 1996, Dawson et al. 2000, Serra et al. 2007). Unfortunately, these interesting studies examining tradeoffs in feather quality and molt speed did not determine whether the loss in feather quality was due to the rate at which individual feathers grow, or to the number of feathers grown simultaneously. Increased feather growth rate and molt intensity could both result in reduced feather quality, but effects on feather quality could differ dramatically for these two mechanisms.

We suggest that minor variation in the rate of feather growth accounts for differences in structural integrity of the flight feathers. When body-size effects are removed, feather growth rates are slightly higher in species that replace flight feathers nearly simultaneously than in species that replace only a few flight feathers at once and maintain the ability to fly while molting (S. Rohwer et al. 2009). This counterintuitive result suggests that development can proceed faster when tissues are not being used as they are developed (Ricklefs 1973). The apparent lack of a tradeoff between the number of feathers grown simultaneously and feather growth rate suggests that it is not the blood supply of keratin, but the rate at which the collar of the feather follicle can proliferate differentiated keratinocytes that become the rachis, rami, and barbules of the developing feather, that constrains feather growth rate (Lucas and Stettenheim

Table 3. Intraspecific variation in molt duration, primary molt intensity, and feather growth rate for 12 species that have different molt durations because of either experimental manipulations or natural geographic or seasonal variation in primary molt duration; 8 of these 12 species had measures of feather growth rate. Expected-contrast columns indicate whether differences in molt intensity or feather growth rate are in the expected direction to reduce molt durations.

Species	Molt duration (days)		Molt intensity (number of feathers growing simultaneously)		Molt intensity expected contrast	Feather growth rate (mm day⁻¹)		Feather growth rate expected contrast	Notes	References
	Fast	Slow	Fast	Slow		Fast	Slow			
Black-bellied Plover (*Pluvialis squatarola*)	90	125	2.55	1.94	Yes	Similar	Similar	No	Natural	Serra and Underhill 2006
Red Knot (*Calidris canutus*)	77	96	"More"	"Less"	Yes	Similar	Similar	No	Natural	Summers et al. 2009
Ruff (*Philomachus pugnax*)	50–60	110–130	2 or 3	1.3	Yes	NA	NA	NA	Natural	Pearson 1981
Black-capped Vireo (*Vireo atricapilla*)	50	62	2.9	2.5	Yes	NA	NA	NA	Natural	Butler et al. 2008
Willow Warbler (*Phylloscopus trochilus*)	30–35	65–80	3.8	2	Yes	3.01	2.91	Yes	Natural	Pearson 1973, de la Hera et al. 2011
Black-chested Prinia (*Prinia flavicans*)	67	108	2.25	1.93	Yes	2.09	2.02	Yes	Natural	Herremans 1999
Lesser Whitethroat (*Sylvia curruca*)	40.9	47.1	9	7.1	Yes	NA	NA	NA	Experimental	Hall and Fransson 2000
European Starlings (*Sturnus vulgaris*)	92	119	3.23	2.13	Yes	4.70	5.00	No	Experimental	Dawson 2004
Rock Sparrow (*Petronia petronia*)	81	139	2.81	1.47	Yes	2.64	2.77	No	Experiment	Serra et al. 2010
Red-billed Quelea (*Quelea quelea*) [a]	75	124	1.08	1.98	No	3.64	2.61	Yes	Natural	Oschadleus and Underhill 2008
Zebra Finch (*Taeniopygia guttata*) [b]	70–76	88–100	"More"	"Less"	Yes	2.57	1.27	Yes	Experimental	Echeverry-Galvis and Hau 2012
Yellow Warbler (*Setophaga petechia*)	40	44.5	"More"	"Less"	Yes	NA	NA	NA	Natural	Ryder and Rimmer 2003

[a] We used feather growth rates that we measured directly from museum specimens rather than those presented in Oschadleus and Underhill (2008).
[b] We considered molt intensity to generally increase across all feather groups presented in Echeverry-Galvis and Hau (2012).

1972, Prum 1999). We know of no investigations of constraints on the rate of feather growth.

Feather growth rate is closely associated with both body size (Fig. 1) and feather size (Fig. 2; and see de la Hera et al. 2012). With size effects removed, the limited variation in molt duration explained by feather growth rate (Fig. 3A) suggests strong stabilizing selection for feather growth rate that best resolves the conflict between feather quality and the speed at which feathers grow. Birds that increase the rate at which feathers grow may suffer disproportionate costs in feather quality, to the detriment of annual survival and reproductive success, compared with birds that pay the cost (only during the molt) of growing high-quality feathers at a slower rate.

Flexibility in molt intensity.—The importance of molt intensity in explaining variation in the duration of primary replacement has been noted in comparative studies before, but these studies did not address the relative importance of molt intensity and feather growth rate (Prater 1981, Jenni and Winkler 1994). The number of flight feathers replaced simultaneously shows great variation both among and within species and even within individuals in different years. In some species of hornbills, females replace their flight feathers simultaneously during incubation and the early stages of nestling care, whereas males replace flight feathers sequentially, maintaining the ability to fly and provision both the molting

female and offspring (Kemp 1995). Individual Greater Flamingos (*Phoenicopterus ruber roseus*) can alternate between sequential and simultaneous molts between years (Studer-Thiersch 2000). Similarly, several species show geographic or seasonal variation in the number of feathers they replace simultaneously (Table 3). Molt intensity seems to be a labile trait within species, and varying molt intensity appears to be the principal way that feather renewal is fit into the annual cycle while maximizing breeding attempts or meeting the time constraints of seasonal environments.

For birds that fly while molting, the cost of replacing more flight feathers simultaneously has been mitigated by complex modes of flight feather replacement that separate gaps in the wing,

Table 4. Effects of body mass, primary molt intensity, and feather growth rate on the duration of primary molt. Statistics include 52 comparisons of primary molt intensity and feather growth rate shown in Figure 3 and exclude simultaneous molters.

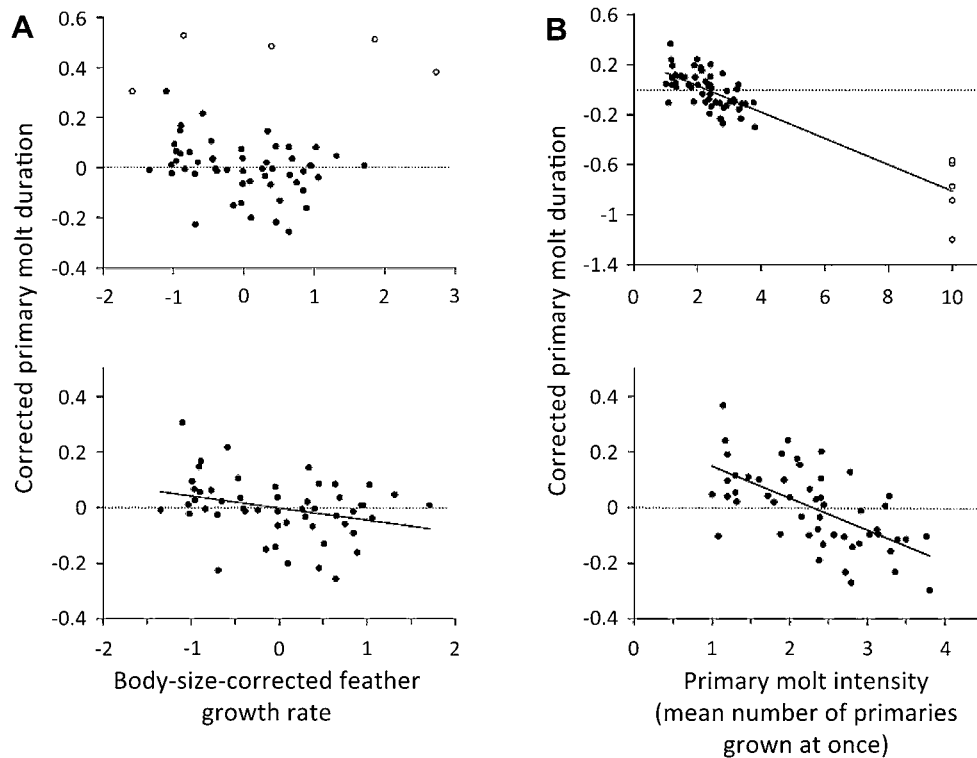|	Slope	SE	t	P
Body mass	0.281	0.039	7.126	<0.00001
Intensity	−0.147	0.0219	−6.728	<0.00001
Feather growth rate	−0.054	0.0223	−2.429	0.0189

FIG. 3. Effects of feather growth rate and primary molt intensity on primary molt duration. (A) Corrected primary molt duration for 52 comparisons from 43 species regressed on body-size-corrected primary feather growth rates. Corrected primary molt duration is the residuals of a general linear model (GLM) that controls for the contributions of body mass and primary molt intensity to primary molt duration; negative numbers along the y-axis represent rapid molts and positive numbers represent slow molts. Circles in the upper plot are species that replace their primaries simultaneously; these species were not included in the statistical analyses. There is a relationship between feather growth rates and molt duration (lower plot without simultaneous molters; Table 4) showing that increasing feather growth rates reduces the duration of molt. This relationship disappears when simultaneous molters are included in the model (upper plot). (B) Corrected primary molt duration for the same 52 comparisons for 43 species regressed on primary molt intensity. Corrected molt duration is the residuals of a GLM that controls for the effects of body size and feather growth rates on primary molt duration. The upper plot included 5 species of simultaneous molters (circles) to illustrate cases of extreme primary molt intensity; these species were not included in our statistical analyses. As molt intensity increases, molt duration decreases (lower plot; Table 4), and this relationship becomes even stronger if simultaneous molters (the circles in the lower right-hand quadrant of the upper plot) are included in the model.

apparently to reduce their aerodynamic costs (Hedenström and Sunada 1999), and allow large birds to renew flight feathers frequently enough to minimize breeding sabbaticals forced by worn feathers (Rohwer et al. 2011). Adults of many large birds feature stepwise replacement of the primaries, whereby several separated

waves of feather replacement proceed through the primaries simultaneously (Stresemann and Stresemann 1966). A few groups (albatrosses, falcons, and parrots) have broken the primaries into two replacement series, which separates gaps in molting wings and also allows feathers to be replaced on different schedules, with some routinely retained for 2 years (Langston and Rohwer 1996). These complex modes of molt that increase the number of feathers grown simultaneously while minimizing the aerodynamic costs of replacing several feathers at once (Ashmole 1968, Tucker 1991) apparently have originated in many independent lineages.

The paradox of ptilochronology.—It seems puzzling that ptilochronology, the measurement of feather growth rate (Grubb 2006), has been used successfully to infer individual condition when feather growth rate appears to be constrained by body mass and feather size (S. Rohwer et al. 2009, de la Hera et al. 2012). Yet numerous empirical studies suggest that rates of feather growth are well associated with individual quality within populations (Hill and Montgomerie 1994, Doucet 2002). On one hand, variation in the growth rate of flight feathers seems so constrained that it would be unlikely to provide a reliable index of environmental or individual

TABLE 5. ANOVA table showing the variance in primary molt duration explained by body mass, primary molt intensity, and feather growth rates. Statistics exclude simultaneous molters from the analysis and include 52 comparisons for which data on duration, intensity, and feather growth rate are available.

Variable	Sum of squares	Percent explained without body mass
Body mass	0.583	–
Intensity	0.888	60.0
Feather growth rate	0.065	4.4
Residual	0.528	35.6
Total	2.064	100.0

quality. On the other hand, small differences in feather growth rate could reflect large differences in environmental or individual quality. There is variation around the allometric lines relating feather growth rates to body mass (Fig. 1; and see fig. 1 in S. Rohwer et al. 2009) and feather size (de la Hera et al. 2012), and it seems unlikely that this variation is entirely due to measurement error, particularly because tropical species tend to grow their feathers more slowly than temperate species (V. G. Rohwer and S. Rohwer unpubl. data).

As feathers develop, keratinocytes differentiate from the collar cells, fill with keratin, and are extruded from the follicle as additional keratinocytes differentiate below them. As keratinocytes lose contact with the nourishing feather pulp, they die and become the structural elements of the nonliving feather. New models for the development of feathers suggest that the axial rate of feather growth is not constant, but that the absolute rate of differentiation of the central rachis and of the barbs making the feather vein is constant (Prum 1999, Prum and Williamson 2001). Harris et al. (2005) further show that the number of barb ridges is a remarkably linear function of the circumference of the ring of collar cells that generate the feather, apparently because more barb ridges must be generated to make wider feathers. The ~0.5 relationship between the allometric coefficients for feather length (1/3 power scaling) and feather growth rate (about 1/6 power scaling) suggest that the two-dimensional structure of flight feathers is produced from a linear structure (S. Rohwer et al. 2009), and the tight linear relation between the number of barb ridges and the circumference of the ring of collar cells (Harris et al. 2005) suggest that it is the circumference of this ring of collar cells that sets the upper limit of feather growth rate.

Feather development involves alternately turning on and off genes that result in the development and differentiation of the keratinocytes (Harris et al. 2005), a developmental process that, if accelerated, may sacrifice feather quality. This hypothesis is supported by the minimal variance in molt duration that is explained by feather growth rate and by the similarity of flight feather growth rates in sequential and simultaneous molters (S. Rohwer et al. 2009). Thus, birds in good condition probably cannot exceed the maximum rate at which keratinocytes can be differentiated, but birds facing greater metabolic demands or birds in poor condition may, nonetheless, be able to produce reasonably high-quality feathers by growing them more slowly and spending more time in molt (White et al. 1991, Echeverry-Galvis and Hau 2012). If birds in poor condition or in poor habitats can grow feathers slowly without much loss in feather quality, then, by suffering the energetic and aerodynamic costs of molting over a longer period, they can largely avoid the costs of low-quality feathers that must be worn until the next molt. We suggest that it is these small decreases in the rate of feather growth that make ptilochronology a useful tool.

Synopsis.—To our knowledge, this is the first comparative analysis of how the duration of the primary molt is affected by primary growth rate and primary molt intensity. Across 52 comparisons of 43 species, growing more feathers simultaneously explained 60.0% of the variation in molt duration, and flight feather growth rate explained 4.4% of this variation. Although body size and feather size constrain the rate at which feathers grow (S. Rohwer et al. 2009, de la Hera et al. 2012), we suggest that limits on feather growth rate lie at the follicular level. Increasing feather growth rate apparently would generate feathers of lower quality, with fitness costs that would be born throughout the life of those feathers (Nilsson and Svensson 1996, Dawson et al. 2000, Serra et al. 2007). Surprisingly, however, the fitness costs of growing many feathers simultaneously seem to be confined primarily to the period of active feather growth because feather quality seems not to be sacrificed by growing more feathers simultaneously (S. Rohwer et al. 2009). This means that birds are relatively free to adjust the number of flight feathers they grow simultaneously when the time available for molting is constrained by other life-history demands.

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