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A PRIMER ON SUMMARIZING MOLT DATA FOR FLIGHT FEATHERS

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Abstract.   Once established with reliability, the rules of flight feather replacement become an important component of comparative life-history studies. Here I illustrate the form of tables that should be used to describe the pattern and intensity of flight feather molt. Using a subset of original data summarizing primary, secondary, and rectrix molt in Western Kingbirds (*Tyrannus verticalis*), I show how to assign scores indicating direction of replacement and points where waves of molt started or will stop. Combining these scores across birds yields a molt summary table, the starting point for determining the rules of feather replacement. This raw summary table is then iterated to show breaks between molt series and how summary scores around these breaks are reassigned to acknowledge series breaks. Molt summary tables also give sample sizes, because the rules of flight feather replacement cannot reliably be inferred unless birds in active molt are available for all the feathers being considered.

Key words: flight feather replacement rules, molt tables, primary molt, rectrix molt, secondary molt, Western Kingbird.

Una Introducción Concisa al Tema de Cómo Resumir Datos de la Muda para las Plumas del Vuelo

Resumen.   Una vez que son establecidas confiablemente, las reglas de reemplazo de las plumas del vuelo representan un componente importante en los estudios comparativos de las historias de vida. Aquí muestro la forma de las tablas que deben ser usadas para describir el patrón y la intensidad de la muda de las plumas del vuelo. Usando una submuestra de datos originales que resume la muda de las primarias, secundarias y rectrices en *Tyrannus verticalis*, muestro como asignar puntajes indicando la dirección de reemplazo y los puntos de inicio o de finalización de las oleadas de muda. La combinación de estos puntajes entre aves proporciona una tabla de resumen de la muda, que representa el punto de partida para determinar las reglas de reemplazo de las plumas. Esta tabla cruda de resumen luego es iterada para mostrar cortes entre las series de muda y cómo los puntajes resumidos alrededor de estos cortes son reasignados para determinar los cortes en las series. Las tablas de resumen de la muda también proporcionan el tamaño de muestra, porque las reglas de reemplazo de las plumas del vuelo no pueden ser inferidas de modo confiable a menos que las aves con muda activa estén disponibles para todas las plumas en consideración.

Comparative studies of avian molt cycles simply demand better data than are presently being published in most descriptions of flight feather replacement (Bridge 2006). My goal with this commentary is to provide a framework for reporting and inferring the rules of flight feather replacement based on records representing snapshots of the molt status of individual birds. These rules tell us: (1) how the wing is broken into groups of feathers, or "molt series" (recognized by coordinated replacement of the feathers within these groups; Yuri and Rohwer 1997), (2) how replacement proceeds within each of the molt series with respect to the sequence (usually direction) of feather replacement, (3) whether multiple waves of replacement move through the series simultaneously (Shugart and Rohwer 1996, Filardi and Rohwer 2001), (4) how different molt series are organized with respect to sequence of activation within molt cycles (Yuri and Rohwer 1997), and (5) the frequency of feather replacement across molt cycles (Edwards and Rohwer 2005).

Of course, the rules of flight feather replacement could easily be determined by reexamining individual birds at multiple points during their molt; further, if these same individuals could be followed through multiple molts, we would know whether replacement rules were fixed for an individual's life or varied from molt to molt. But data on flight feather replacement usually represent snapshots of single individuals in different stages of molt that were recorded from specimens, released birds (Ginn and Melville 1983), or even photographs (Snyder et al. 1987). Thus, molt series are usually inferred by the direction in which feather replacement proceeds, by closely linked replacement between neighboring pairs of feathers, and by identifying feathers that mark the beginning or end of a replacement series (Underhill 1986, Filardi and Rohwer 2001). Correctly identifying a molt series is essential to correctly interpreting the mode of flight feather replacement for that series. For example, if the primaries constitute a single molt series, then two waves of primary replacement suggest stepwise molting (Stresemann and Stresemann 1966, Rasmussen 1988, Shugart and Rohwer 1996), but two waves of primary replacement also can occur when the primaries are organized into two independently activated molt series, an adaptation that increases flexibility in the frequency of feather replacement (Langston and Rohwer 1996, Edwards and Rohwer 2005).

For large birds, describing the rules of secondary replacement is particularly problematic because their many secondaries are inaccessible on traditional study skins. Thus, for most birds, we know little about how full molts of the primaries and secondaries are related to size, to differential rates of feather wear across the wing, and to breeding ecology. Laysan (*Phoebastria immutabilis*) and Black-footed Albatrosses (*P. nigripes*) are exceptions because Edwards and Rohwer (2005) used extended wings to show that the 10 primaries and 28–31 secondaries are divided into at least four molt series, and that molt is initiated more frequently in the outermost and innermost molt series to accommodate higher rates of feather wear in those series; moreover, activating any of the three series containing secondaries adds no more time to the flight feather molt than replacing just the outer primaries (Edwards and Rohwer 2005).

As body size increases, the time required to replace all the primaries increases dramatically, with the result that complete primary molts require a large fraction of the annual cycle for large

birds. The reason for this is that the growth rate for primaries scales with body mass (M) as $M^{0.170}$, while the summed lengths of the primaries scales with mass almost twice as fast, as $M^{0.314}$ (SR et al., unpubl. data). Because these allometric regression lines diverge, larger birds need much more time to replace all their primaries than smaller birds: on average, a 10 g bird would need 179 days to replace all its primaries one feather at a time, a 100 g bird would need 242 days, a 1000 g bird would need 346 days, and a 10 000 g bird would need 482 days. All birds that fly while molting reduce these time demands by replacing more than one primary concurrently per molt wave; further, many large birds replace their primaries in multiple waves, which simultaneously reduces the size of molt gaps (because adjacent flight feathers overlap each other) and increases the number of primaries growing at the same time (Ashmole 1968). Nonetheless, because of the time required to replace all flight feathers, species that fly while molting and that are larger than about 1000 g regularly have incomplete primary molts (SR et al., unpubl. data).

Thus, flight feather molt is of fundamental importance to many aspects of avian biology. The time required to replace flight feathers drives breeding frequencies (Ashmole 1968, Langston and Rohwer 1996, Edwards 2008), and estimating the time required to replace the feathers of a flight feather molt series (Pimm 1976) requires knowing what feathers constitute a molt series and how those feathers are replaced, neither of which we know for many species. Further, asymmetries in flight feather replacement have been shown to reduce survival (Brommer et al. 2003), and these asymmetries are generated by the incomplete molts that are associated with multiple waves of flight feather replacement in large birds that fly while molting. Finally, for large birds that replace the primaries in a single wave, evolving larger size eventually becomes impossible without a corresponding transition to replacing the primaries in multiple waves or to molting the flight feathers simultaneously (SR et al., unpubl. data).

Inferring the rules of flight-feather replacement from single observations has proven challenging because data on flight feather replacement are difficult to summarize and interpret. Thus, my students and I developed molt summary tables. With these tables we attempted to summarize raw data quantitatively, to simplify interpretation, and to facilitate the presentation of inferences used to define boundaries between molt series (Langston and Rohwer 1995, Shugart and Rohwer 1996, Yuri and Rohwer 1997, Filardi and Rohwer 2001). Unfortunately, these tables seem to have been too complicated to have become popular, and even other experts on molt have failed to extract data from these tables that would have tested their own alternative interpretations of molt rules (Howell 2006, Rohwer and Edwards 2006). These failures of our earlier molt tables inspired me to devise and present a simpler way for summarizing, presenting, and interpreting data on flight feather replacement. Hopefully these new summary tables, and particularly their new, iterated, versions, will make the presentation and interpretation of data on flight-feather replacement both more reliable and more transparent.

GENERATING DATA TABLES FROM INDIVIDUAL WINGS

To show how original data tables on flight feather molt can be summarized, I present in Table 1 the raw data for 10 of the 58 molting adult Western Kingbirds (*Tyrannus verticalis*) used to generate my full data set. I present this subset of the raw data to illustrate how molt summary tables (Table 2) are generated

from the original data table and then interpreted through a series of iterations. The process involves the following fundamental steps.

STEP 1: CLASSIFYING FEATHERS AS NEW, OLD, OR GROWING

This is an easy step in birds that have complete molts, because feathers may be categorized as new (which can also be scored as 1), old (0), or growing (scoring described below). In large species with incomplete molts, assigning feathers to year-classes is important and difficult because the flight feathers wear differentially across the wing (Langston and Rohwer 1995, Edwards and Rohwer 2005). For these species, the "new" categorization becomes a year-class, denoting replaced in the latest (or current) molt (1), replaced in the molt before last (2), or replaced in a molt that took place about two to three years earlier (3). Feather age categories must be interpreted by when in the annual cycle the scores were assigned. If the assignments were made during an active molt, then 1 indicates a new feather that has just been grown, but if the assignments were made shortly before the annual molt, then the 1 represents a feather about a year old. In the tables presented here I simply use "new" or "old" as descriptors, because all of these kingbirds were molting and because adults replace all flight feathers each year.

STEP 2: SCORING GROWING FEATHERS

Without information on growing feathers, it is impossible to distinguish between simple, stepwise and multiple series molting; thus, scoring growing feathers is critically important. If the rate at which feathers grow is approximately constant across the wing, as it is in Laysan and Black-footed Abatrosses (Langston and Rohwer 1995), the relative lengths of growing feathers indicates their sequence of replacement. Rohwer (1986) suggested scoring growing flight feathers as fractions of their full length because fractional scores are easy to assign and usually accurate enough to avoid interpretive problems. However, fractional scores can result in errors in assigning the direction of replacement when adjacent feathers differ considerably in their full length (e.g., S7–S9). Thus, Howell (2006) transformed the fractional lengths presented by Langston and Rohwer (1995) for growing primaries of albatrosses into mm of emerged feather. This problem was recognized and treated appropriately by Langston and Rohwer (1995:3), but I agree with Howell (2006) and advocate recording lengths for growing feathers when there is doubt about which of a pair of growing feathers was lost first. I score missing feathers as 0.01, simply to avoid confusing them with old feathers. I score feathers that are almost fully grown or that are fully grown but retain sheathing at their bases as 0.99 so they can be included or excluded in comparisons of adjacent feathers, as appropriate. Excluding scores of 0.95–0.99 from directional comparisons is sometimes important, because the rate at which feathers grow slows as they near their full length (Jenni and Winkler 1994), making it possible for a longer feather scoring 0.90, that was shed later than a shorter feather scoring 0.95, to appear to have been shed earlier.

STEP 3: MAKING THE RAW DATA TABLE

Molt data tables, which are usually too bulky to merit publication, provide the information needed to generate molt summary tables. In this kingbird example (Table 1), all growing feathers are assigned fractional scores and all full-length feathers assigned descriptive scores of new or old. Note that if the table were

TABLE 1. Ten exemplar cases of scoring feather states for primaries and secondaries from the raw data on 58 molting Western Kingbird specimens. Lines with specimen numbers present the status of all feathers in that wing as old, new, or growing (expressed as fractions of full length). Entered in the line above each specimen are notations that are counted to quantitatively summarize the rules of feather replacement in the molt summary table (Table 2). These notations are nodal (N) and terminal (T), which are placed over feather scores, and three indicators of the direction of feather replacement, which are placed between appropriate pairs of feathers: distal replacement ($\rightarrow$), proximal replacement ($\leftarrow$), or A for ambiguous direction (when adjacent growing feathers are the same length).

UWBM[a] specimen number	Secondaries									Primaries									
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
77589	N$\rightarrow$ 0.01	old	old	old	old	old	old	old	$\leftarrow$ old	N$\rightarrow$ 0.90	$\rightarrow$ 0.80	$\rightarrow$ 0.01	$\rightarrow$ old	old	old	old	old	old	old
77673	old	$\leftarrow$ N$\rightarrow$ 0.01	$\rightarrow$ old	old	old	old	old	old	$\leftarrow$ old	N A 0.80	N$\rightarrow$ 0.80	$\rightarrow$ 0.65	$\rightarrow$ 0.20	old	old	old	old	old	old
77726	N$\rightarrow$ 0.80	N$\rightarrow$ 0.10	$\rightarrow$ old	old	old	old	old	$\leftarrow$ old	$\leftarrow$ 0.30	new	new	$\rightarrow$ 0.90	$\rightarrow$ 0.80	$\rightarrow$ 0.40	$\uparrow$ old	old	old	old	old
77824	old	N$\rightarrow$ 0.20	$\rightarrow$ old	old	old	old	$\leftarrow$ old	$\leftarrow$ 0.10	$\leftarrow$ 0.75	new	$\uparrow$ new	$\uparrow$ 0.95	$\uparrow$ 0.70	$\uparrow$ 0.60	$\uparrow$ 0.30	$\uparrow$ 0.20	$\uparrow$ old	old	old
77837	new	new	new	new	T $\leftarrow$ old	$\leftarrow$ 0.40	$\leftarrow$ 0.95	new	new	new	new	new	new	new	new	$\uparrow$ 0.90	$\uparrow$ 0.50	$\uparrow$ 0.20	T 0.05
77838	new	new	new	old	$\leftarrow$ old	$\leftarrow$ 0.30	0.95	new	new	new	new	new	new	new	new	$\uparrow$ 0.90	$\uparrow$ 0.60	$\uparrow$ 0.40	T 0.20
77890	new	new	new	$\uparrow$ 0.80	T $\leftarrow$ 0.50	$\leftarrow$ 0.90	new	new	new	new	new	new	new	new	new	new	$\uparrow$ 0.80	$\uparrow$ 0.60	T 0.40
77954	new	new	new	T $\leftarrow$ old	$\leftarrow$ 0.20	$\leftarrow$ 0.30	0.90	new	new	new	new	new	new	new	new	new	$\uparrow$ 0.30	$\uparrow$ 0.20	T 0.10
80322	$\leftarrow$ N$\rightarrow$ 0.50	N$\rightarrow$ 0.90	$\uparrow$ 0.40	old	old	old	$\leftarrow$ old	$\leftarrow$ 0.01	$\leftarrow$ 0.80	new	new	new	new	$\uparrow$ 0.90	$\uparrow$ 0.50	$\uparrow$ 0.01	$\uparrow$ old	old	old
84652	N A N$\rightarrow$ 0.30	N$\rightarrow$ 0.25	old	old	old	old	old	$\leftarrow$ old	$\leftarrow$ 0.20	new	$\uparrow$ new	$\uparrow$ 0.95	$\uparrow$ 0.80	$\uparrow$ 0.20	$\uparrow$ 0.01	$\uparrow$ old	old	old	old

[a] UWBM = University of Washington Burke Museum.

TABLE 2. Count summary of the raw molt scores (examples in Table 1) for primaries and secondaries for the sample of 58 Western Kingbird specimens that were molting primaries, secondaries, or rectrices; and iteration of the raw summary data for the primaries and secondaries. Iteration adjusts the scores around P1–S1 and S5–S6 to recognize that the wing quills are split into three molt series, P1–P10, S1–S5, and S6–S9, separated by the gray bars.

	Secondaries									Primaries									
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Raw summary data																			
Nodal	9	16	0	0	0	0	0	0	0	11	5	0	0	0	0	0	0	0	0
Direction ←	16	0	0	0	1	15	25	27	29	9	9	0	0	0	0	0	0	0	0
Direction →	0	26	21	21	15	0	0	0	0	0	25	25	24	26	26	33	30	22	0
Direction ?	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Terminal	0	0	0	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	20
Number growing	18	17	12	9	7	15	19	15	18	11	15	22	21	21	20	22	22	20	19
Iterated summary data																			
Nodal	9	16	0	0	0	0	0	0	0	11	5	0	0	0	0	0	0	0	0
Direction ←	16	0	0	0	0	15	25	27	29	9	9	0	0	0	0	0	0	0	0
Direction →	0	26	21	21	15	0	0	0	0	0	25	25	24	26	26	33	30	22	0
Direction ?	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Terminal	0	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	20
Number growing	18	17	12	9	7	15	19	15	18	11	15	22	21	21	20	22	22	20	19

treating a species in which feathers were retained through two or more molts, full-length feathers would be assigned to year-classes, as detailed above. In the line above the raw data entry for each bird, we now make the summary assignments: nodal (N), terminal (T), and direction of replacement. These notations are then summarized as counts for the entire table to give the molt summary table (Table 2).

Nodal feathers initiate a wave of feather replacement, while terminal feathers mark the end of a wave of feather replacement. A feather qualifies as nodal if it is growing and fits any of the following three conditions illustrated in Table 1: nodal feathers may be surrounded by old feathers (e.g., UWBM 77824, S8); nodal feathers may have one old neighbor and one growing neighbor that is shorter than the focal feather (e.g., UWBM 77598, P1); or nodal feathers may be surrounded by growing feathers, both of which are shorter than the focal feather (e.g., UWBM 80322, S8). Terminal feathers are defined in ways similar to but the reverse of nodal feathers (e.g., UWBM 77837, S5 and UWBM 77890, S5; Yuri and Rohwer 1997). Edwards and Rohwer (2005) provide an elaborate quantitative approach for identifying terminal feathers for molt series that are bounded not by the end of the wing, as for the primaries in kingbirds (e.g., UWBM 77838; Table 1), but by the beginning or end of another molt series that may not have been activated in the current episode of molt.

In large birds for which molts are often incomplete, nodal feathers do not always mark the beginning of a molt series and terminal feathers do not always mark the end of a molt series. When primary replacement is incomplete, as in most birds that molt in a stepwise fashion, nodes of molt initiation and termination will be scattered throughout the primaries (Shugart and Rohwer 1996). For example, if all the primaries belong to a single molt series and if primary replacement is stepwise with distal replacement (from P1 to P10), then only P1 will mark the beginning of the primary molt series (Rasmussen 1988, Shugart and Rohwer 1996, Filardi and Rohwer 2001) and will qualify as a "dominant node." Edwards and Rohwer (2005) provide a summary of the corrections needed to look for dominant nodes when the annual probability of feather replacement varies across the wing. Feather skipping (wherein some feathers in a molt series are not replaced when other feathers that are farther downstream in that same series are replaced), which Edwards and Rohwer (2005) showed to be common in the inner primaries and outer secondaries of Laysan and Black-footed Albatrosses, may also generate nodes and termini that do not mark the beginning or end of a molt series.

Direction of replacement is the final key piece of information that must be summarized in the line above the raw data for each bird. I advocate restricting directionality assignments just to adjacent pairs of feathers so that they tell us for each appropriate feather pair whether molt is proceeding distally or proximally (Table 1). In previous summary tables I inferred direction of replacement by comparing each growing feather to both of its neighbors (Langston and Rohwer 1995, Yuri and Rohwer 1997). However, comparing focal feathers with both neighbors created problems at the ends of the wing where there was only one neighbor and problems throughout the wing when the two neighbors gave contradictory information about direction. I scored the latter cases as "ambiguous direction" (Langston and Rohwer 1995) and used them to help identify nodal and terminal feathers. Except for growing pairs of feathers that are the same length, "ambiguous direction" is completely avoided by pairwise directionality scoring. The rationale for using both neighbors in earlier papers was that the sum of all entries (nodal, terminal, proximal direction, distal direction, or ambiguous direction) gave the number of

growing feathers at each locus (Langston and Rohwer 1995, Shugart and Rohwer 1996, Yuri and Rohwer 1997). However, sample sizes for growing feathers can easily be provided in molt summary tables from direct counts (Table 2).

A critical decision is whether directionality should be assigned only between adjacent growing feathers or between growing feathers flanked by old or new feathers. Many species molt so slowly that adjacent growing pairs are too rare to provide enough data (e.g., UWBM 77589, P2–P3; Table 1); therefore, I advocate including directionality scores between both adjacent growing feathers and between growing and new or old feathers (e.g., UWBM 77726, P2–P3; UWBM 77726, P5–P6; Table 1). Including adjacent new or old feathers tends to introduce directionality scores across boundaries between adjacent molt series (see the treatment of the P1–S1 boundary below). Directionality scores should not be assigned to adjacent new and old feathers because correctly inferring the rules of flight feather replacement requires samples of wings in active molt.

STEP 4: GENERATING SUMMARY TABLES FOR INFERRING REPLACEMENT RULES

At this point, each molting wing is summarized in two lines in the molt data tables. The raw data lines present feather ages and fractional scores for growing flight feathers, and the line above each data row assigns status as nodal or terminal and indicates the direction of replacement between adjacent feather pairs where at least one of the pair was growing (Table 1). It is now simple to tabulate the frequency of each directional, nodal, or terminal occurrence in a separate molt summary table. I present these summary data for the primaries and secondaries in Table 2, and for the rectrices in Table 3. The counts in these summary tables are tedious to make and to change each time scoring is corrected, so obtaining the summary counts should be automated using the COUNTIF function in Excel.

STEP 5: INTERPRETING SUMMARY DATA USING ITERATIONS—PRIMARIES AND SECONDARIES

With molt summary tables, groups of feathers that form separate molt series can be identified by a combination of breaks in the direction of feather replacement and locations of feathers that

frequently score as nodal or terminal. In Western Kingbirds, there are three molt series in the primaries and secondaries. As with most passerines, the primaries constitute a single molt series and are replaced from P1 distally to the outermost primary (P10). The summary table illustrates this in several ways. First, P1 is frequently nodal and P10 is always terminal. Because P1 and P2 are lost in quick succession, or even simultaneously (e.g., UWBM 77673; Table 1), P2 also shows up as nodal, although at a far lower frequency than P1 (Table 2). Thus, we may infer that P1 marks the beginning of this molt series, but the contradictory information about the sequence of replacement of P1 and P2 is fully revealed in the summary table. Importantly, every other adjacent pair of primaries suggests proximal to distal replacement; the lack of discontinuity in direction of replacement further suggests, but does not prove, that the primaries are all part of a single molt series. Given the simple and consistent primary replacement rules for passerines, none of this is surprising, but it is helpful to know that this conclusion is based on reasonable samples of growing feathers for most of the primaries (Table 2). When there are gaps in the data, the conclusion that all the primaries constitute a single molt series could be questioned. In other orders, such as falcons (Miller 1941), albatrosses (Langston and Rohwer 1995), parrots (Forshaw and Cooper 1989), owls (Forsman 1981), and some tree swifts (SR and L. Wang, unpubl. data), there are two molt series in the primaries.

The secondaries of Western Kingbirds are divided into two molt series, S1–S5 and S9–S6. This inference is slightly more difficult to make for several reasons. First, S1 never scores as nodal in the raw data summary because molt always starts in the primary series well before it initiates at S1 (e.g., UWBM 77589; Table 1). At the nodal boundaries between molt series, where feathers are replaced in opposite directions, only one of the two nodal feathers can score as nodal. The other must be inferred to be nodal. In kingbirds, the direction of feather replacement is strongly proximal from S1 to S5, so we know that S1 is the nodal feather that initiates molt in the outer secondaries. To make such inferences clear, I advocate presenting derivative molt summary tables that have been iterated (Table 2, 3).

Iterated tables do two things. First, they draw attention to series boundaries, which are difficult to see in raw summary tables because the series are inappropriately linked by directionality

TABLE 3. Count summary of the raw molt scores for rectrices from the sample of 58 Western Kingbird specimens that were molting primaries, secondaries, or rectrices; and iteration of the raw summary data for the rectrices, which adjusts the R5–R6 scores to recognize that the rectrices are split into two molt series, R1–R5, and R6, separated by the gray bar.

	R1	R2	R3	R4	R5	R6
Raw summary data						
Nodal	19	1	0	0	0	12
Terminal	2	0	0	0	13	15
Direction →	18	24	26	25	14	
Direction ←	2	1	0	0	12	
Direction ?	1	0	2	1	1	
Number growing	21	17	25	25	22	24
Iterated summary data						
Nodal	19	1	0	0	0	27
Terminal	2	0	0	0	27	
Direction →	18	24	26	25		
Direction ←	2	1	0	0		
Direction ?	1	0	2	1		
Number growing	21	17	25	25	22	24

assignments. Second, they focus attention on revisions in the summary table that are made to accommodate knowledge about series boundaries. In the summaries presented in Table 1 and Table 2, directionality was assigned to P1–S1. Thus, the first iteration recognizes S1 as nodal for the secondary series S1–S5, and moves the 29 proximal directionality scores between P1 and S1 to scores of nodal for S1 (Table 2). Removing the directionality scores between P1 and S1 is appropriate because directionality scores are intended to record the direction of feather replacement within a molt series, and not the sequence with which molt is activated in different series. To draw attention to these inferences, I find shading columns that represent breaks between molt series in iterated tables a useful convention; this makes reassignments of raw scores easy to see and highlights inferences that readers should view critically.

The second iteration, also shown in Table 2, is based on inferring that S5 is the terminal feather in the outer series of secondaries. This inference is slightly more challenging, because the direction of replacement converges in the two secondary molt series. Consequently, S5 scores as terminal in some birds (e.g., UWBM 77890; Table 1), while S6 scores as terminal in other birds (e.g., UWBM 77954; Table 1), depending on which was the last feather to be lost. The directionality data in Table 2, however, reveal S6 to be terminal for the inner secondary series and S5 to be terminal for the outer secondary series. This follows because directionality is strongly proximal at S3–S4 and S4–S5, but strongly distal at S8–S7 and S7–S6, while directionality is mixed between S5 and S6. Mixed directionality occurs when one series does not always finish replacement before the other. For this iteration, also shown in Table 2, the nine distal directionality scores for S5–S6 are changed to terminal for S6 and the single proximal directionality score for S5–S6 is changed to terminal for S5, resulting in both S5 and S6 receiving 10 scores of terminal. That S5 receives more terminal scores than S6 in summary Table 2 simply reflects the fact that S6, which is part of a shorter series, is usually replaced before S5 (e.g., UWBM 77890; Table 1).

It is possible that recapture studies of molt would reveal variability among individuals in whether S5 or S6 is terminal for the outer secondary series, but the data in Table 2 do not suggest this to be the case. Further, a single specimen (UWBM 77837; Table 1) refutes including S6 in the outer series of secondaries (as is often reported for passerines). In this specimen S6 is new, S5 is old, and S4 is less than half grown. That S6 is grown but has not stimulated the loss of S5 means that S6 is the terminal feather of the inner secondary molt series (S9–S6). The discovery that S6 is part of the inner series of secondaries in Western Kingbirds varies from the situation in many European passerines, where S1–S6 constitute the outer series of secondaries (Jenni and Winkler 1994). However, Miller (1928) suggested that S6 was part of the inner series of secondaries for Loggerheaded Shrikes (*Lanius ludovicianus*).

As is often the case in passerines, directionality is variable between S9 and S8, with 16 cases of proximal direction (e.g., UWBM 77673; Table 1), eight cases of distal direction (e.g., UWBM 77726), and one case of ambiguous direction (UWBM 84652), where the growing feathers were of equal length even though the fractional scores suggested distal directionality. Apparently S8 and S9 are about equally sensitive to the stimulus that initiates molt in the inner secondaries, with the result that if molt initiates at S8, it then moves in both directions. Nonetheless, the dominant direction of replacement in the inner secondaries is distal. Because conflicts in direction are so frequent between S8 and S9 (Table 1), no reassignment of scores is appropriate for this pair of feathers in iterated Table 2.

INTERPRETING SUMMARY DATA: RECTRICES

The six rectrices of Western Kingbirds seem to be divided into two molt series, R1–R5, and R6 as its own series. This is easy enough to see in summary Table 3. Directionality is strongly proximal to distal from R1 to R5, although there are a few exceptions between R1 and R2 and R2 and R3 because these pairs are often lost almost simultaneously. But there is considerable ambiguity in direction of replacement between R5 and R6, with R6 lost before R5 about half the time. Thus, R6 constitutes its own unique series, because the growth of R5 does not always stimulate its loss. This interpretation is at odds with the interpretation for most passerines, that R1–R6 constitute a single molt series (Jenni and Winkler 1994); however, R6 was recognized as a unique series in Northern Rough-winged Swallows (*Stelgidopteryx serripennis*; Yuri and Rohwer 1997). It may be significant that both swallows and kingbirds use their tails extensively in aerial turns to capture flying insects, but the functional advantage of R6 often being lost before R5 is unclear.

Recognizing R6 as a single-feather series leads to iterated Table 3, where the 14 cases of distal directionality between R5 and R6 become terminal for R5, and where the 15 cases of R6 being terminal are moved to the nodal column for R6. These changes mean that the 12 proximal and single ambiguous directionality assignments between R5 and R6 should be eliminated because all of the proximal directionality scores arose from cases where R6 was nodal and are already included in the nodal count of Table 3. Of course, as a single-feather molt series, R6 is both nodal and terminal.

SPECIES WITH MORE COMPLEX MOLTS

Summary and iterated molt tables similar to those presented in Table 2 and 3 are especially helpful for species for which feather replacement is more complex, particularly species with stepwise primary replacement (Filardi and Rohwer 2001) and species with multiple molt series in the primaries and secondaries (Langston and Rohwer 1995, Edwards and Rohwer 2005). Unfortunately, previous studies used earlier versions of molt summary tables, where directionality scoring included both neighbors of a growing feather. With the simpler directionality scoring proposed here, those data would have been easier to interpret; further, when the summary table is iterated, the replacement patterns are much easier to see. I should emphasize that the examples presented here are not intended to be a comprehensive catalog of the ways we identify series boundaries. Any sound reasoning can work. Presenting the reasoning is critical and presenting iterated summary tables highlights the inferences used to identify series boundaries.

ASSUMPTIONS AND WEAKNESSES

An implicit assumption I make throughout this paper is that the growth of one feather in a molt series somehow stimulates the replacement of the next feather in that series. However, I am unaware of experimental evidence addressing this issue. How the initiation of molt in different feather series is coordinated is even more perplexing. Here the control seems less precise, as molt in the outer series of secondaries initiates sometime between the loss of P4 and P6 in Western Kingbirds. For stepwise molts, we have no information on how molt reinitiates where it was arrested in the preceding year. These problems of control will surely be far easier to address in species where the rules of feather replacement have been well described. For example, surgically transplanting key pairs of feather follicles, if possible, could lead to

TABLE 4.   Mean number of growing flight feathers per side for the various molt series, tallied according to the outermost growing primary in the 58 kingbird specimens molting primaries, secondaries or rectrices. A dash indicates no data.

Molt series	Outermost growing primary									
	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Primaries	—	2.00	2.50	4.00	3.67	3.80	3.38	2.67	4.00	3.53
Outer secondaries (S1–S5)	—	0.00	0.00	0.00	0.67	1.10	2.25	2.33	1.00	2.00
Inner secondaries (S6–S9)	—	0.00	0.25	0.33	1.00	1.00	1.25	1.33	0.00	0.79
Rectrices (R1–R5 and R6)	—	0.00	0.25	0.33	1.00	3.60	4.57	5.00	4.00	2.32
Sum	—	2.00	3.00	4.67	6.33	9.50	11.45	11.33	9.00	8.63
Outermost growing primary (number of specimens)	0	4	4	3	6	10	8	3	1	19

great advances in understanding the mechanisms of interfollicular coordination of molt, and knowing whether these transplants were between or within molt series surely will be critical to interpreting results.

MOLT INTENSITY

The pace of flight feather replacement varies enormously across passerines, making this an interesting variable for comparative studies. Here, following Yuri and Rohwer (1997), I repropose a simple way to summarize the intensity of molt in the flight feathers by taking advantage of the facts that: (1) the primaries are molted as a single series in passerines, (2) the loss of P1 usually marks the initiation of molt, and (3) the outermost primary is usually regrown after or only shortly before the secondaries and rectrices finish growing, and usually well after the intensity of flight-feather molt has peaked (Underhill 1986).

To generate molt intensity tables, birds are first grouped or “binned” by their outermost growing primary. For each primary bin, one then counts for each bird the number of feathers growing in all the flight-feather molt series, then sums across birds within bins, and finally divides by the number of birds in that bin to get a mean (Table 4). It is then a simple step to plot total flight feather molt intensity against the outermost growing primary. For Western Kingbirds, the mean number of growing flight feathers peaks at almost 12 of the 25 flight feathers when the outermost growing primary is P7 (Table 4; Fig. 1). Peak intensities vary widely across species. For example, the peak intensity across the same set of flight feathers in the more aerial Northern Rough-winged Swallow is 6.8 feathers growing (also when P7 is the outermost growing feather; Yuri and Rohwer 1997). Mean intensities should be presented separately by molt series so that other workers can use them in comparisons appropriate to their own data, often just the primaries. Intensity values can be converted to percentages to account for variation in the number of flight feathers among groups of birds.

Mean intensities may prove useful in interpreting differences among individuals within a population. Because intensity varies systematically across the primary molt cycle, the actual value for an individual should be subtracted from the mean for the appropriate outermost growing primary to obtain a deviation from expected for each molting bird. These deviations can then be plotted as histograms to evaluate how sex or age may affect molt intensity, or they can be regressed on day of year to see if late-molting birds grow more feathers simultaneously than early-molting individuals. Neither of these analyses showed anything of interest for this sample of Western Kingbirds.

In conclusion, the critical points of this paper are that descriptions of the pattern and intensity of flight feather replacement should be accompanied by quantitative molt summary tables, and that interpretations of which feathers constitute a molt series should be accompanied by modified tables (here called iterated summary tables) that correct any inappropriate designations in the raw summary table regarding the direction of feather replacement and of nodal and terminal feathers. The examples I present should make such tables easy to generate.
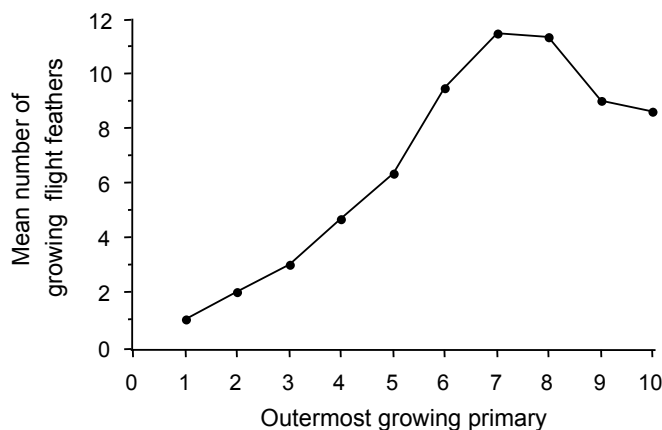
FIGURE 1.   Mean intensity of flight feather molt of Western Kingbirds relative to the outermost growing primary. No specimen was molting only P1 in our data (Table 2); however, molt is not initiated in any other group of flight feathers until P3 is the outermost growing primary (Table 4), so P1 will be the only growing flight feather when it is the outermost growing primary.

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