ECCENTRIC FIRST-YEAR MOLT PATTERNS IN CERTAIN TYRANNID FLYCATCHERS

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Most passerines follow a similar sequence of remex molt, replacement of the primaries commencing with the innermost and proceeding distally, while that of the secondaries (except for the tertials, S7–S9) begins with the outermost and proceeds proximally (Ginn and Melville 1983). During the first-year molts (here defined as all periods of molting before the second prebasic molt), many passerines replace no remiges whereas others replace some or all remiges (Pyle et al. 1987, Jenni and Winkler 1994). "Incomplete" first-year remex molts occasionally result when the typical molting sequence is arrested, the distal juvenal primaries and proximal secondaries (excluding the tertials) being retained. This pattern of incomplete molt is found in several North American passerines, notably, the Phainopepla (*Phainopepla nitens*), Northern Cardinal (*Cardinalis cardinalis*), and Lark Sparrow (*Chondestes grammacus*) (Pyle et al. 1987, Thompson and Leu 1994).

In a few passerine species, incomplete first-year primary molts (and in some cases secondary molts) that do not follow the typical sequence but involve replacement of central or distal primaries in varying patterns have been documented (Jenni and Winkler 1994, Thompson and Leu 1994). These replacement patterns, termed "eccentric" by Jenni and Winkler (1994), are poorly understood. A common eccentric replacement pattern involves renewal of the outer four to six primaries and inner three to five secondaries, feather replacement proceeding distally in the primaries and proximally in the secondaries, as in the typical sequence, but commencing at different points along the wing (Jenni and Winkler 1994; Figure 1). This pattern has been documented in several North American passerines, notably, the Loggerhead Shrike (*Lanius ludovicianus*), Yellow-breasted Chat (*Icteria virens*), and *Passerina* buntings (Miller 1928, Phillips 1974, Thompson and Leu 1994).

While examining specimens of North American tyrannid flycatchers for molt-related age criteria, I found that first-year birds of several species of different genera display eccentric remex-replacement patterns. Depending on the species, replacement of remiges occurs during fall molting periods, spring molting periods, or both. Here I summarize these patterns, and suggest several hypotheses for their occurrence.

MATERIALS AND METHODS

This study was limited to birds collected during their first year. Results were based on data from 589 specimens of 22 north-temperate species examined at the California Academy of Sciences (CAS), Moore Laboratory of Zoology (MLZ), Museum of Vertebrate Zoology (MVZ), and Western Foundation of Vertebrate Zoology (WFVZ). On each specimen I carefully examined the primaries, secondaries, and primary coverts for feather-retention patterns

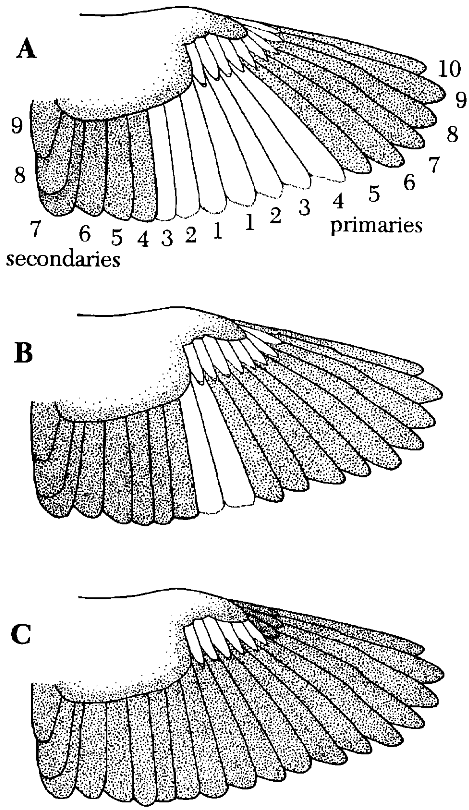

Figure 1. Variation in the eccentric first prebasic molt of the Vermilion Flycatcher, from nine remiges and no primary coverts replaced (A) to all remiges and four primary coverts replaced (C). Shading denotes replaced feathers. Note the difference in shape and wear between retained juvenal primary coverts (inner six feathers in C) and replaced adult primary coverts (outer four feathers in C). In many other tyrannid flycatchers, adults have primary coverts uniformly broad and fresh and are thus separated from first-year birds, with entirely or mostly narrow, pointed, and worn coverts. See also Pyle (1997).

reflecting the extent of previous molts. Birds that had been undergoing active molt when collected (as evidenced by growing or sheathed remiges) were excluded from analyses of extent, as extent could not be determined from these specimens; however, I used specimens in molt for information on the timing and sequence of feather replacement. I examined both wings to assess molt patterns, while all specific data were recorded from the right wings.

During this study I discovered (as confirmed by replacement patterns on specimens collected during active primary molt) that most North American tyrannid flycatchers retain most or all of their juvenal primary coverts until their second prebasic molt and that juvenal and adult (definitive) primary coverts could be identified by differences in shape, color pattern, and relative wear (Figure 1C; see also Pyle 1997). These differences, along with differences in outer primary shape, rectrix shape, feather wear, color of the wing bars, and color of the plumage (Pyle et al. 1987), allowed reliable separation of most first-year from older birds through the second or definitive prebasic molt. Even first-year birds with completely replaced remiges retain five or more inner primary coverts, allowing their accurate separation from adults.

First-year flycatchers show a variety of molting strategies (e.g., Johnson 1963, 1974; Pyle et al. 1987). Remiges can be replaced during the fall (July to November), the spring (March to May), or both (Dickey and van Rossem 1938, Johnson 1963, this study); thus, fall and winter birds can show up to two generations of remiges and spring and summer birds can show up to three generations of remiges. On first-year specimens, I recorded each remex and primary covert as either juvenal, "first fall" (feathers replaced during the fall), or "first spring" (feathers replaced during the spring). After the spring molting period, I distinguished juvenal, first-fall, and first-spring feathers by their relative wear, first-fall feathers being fresher than juvenal feathers but more worn than first-spring feathers.

RESULTS

Among first-year flycatchers, eccentric replacement patterns were found in eight species (Table 1): the Olive-sided Flycatcher (*Contopus cooperi*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), western Willow Flycatcher (*E. traillii brewsteri*, *adastus*, and *extimus*), Vermilion Flycatcher

Table 1 Numbers (Mean and Range) of Consecutive Outer Primaries, Inner Secondaries, and Outer Primary Coverts Replaced on the Right Wing During Eccentric First-Year Molts in Tyrannid Flycatchers

Species	*n*	Inner Primaries[a]	Outer Secondaries[b]	Primary Coverts
Olive-sided Flycatcher	28	7.8 (4–10)	6.9 (3–9)	0.9 (0–4)
Yellow-bellied Flycatcher	12	7.3 (6–10)	7.3 (6–9)	0.0 (—)
Western Willow Flycatcher	37	8.1 (5–10)	7.2 (3–9)	0.0 (—)
Vermilion Flycatcher	82	9.0 (5–10)	8.2 (3–9)	1.3 (0–5)
Western Tropical Kingbird	18	5.3 (5–6)	3.9 (3–6)	0.0 (—)
Cassin's Kingbird	14	1.7 (0–5)	3.7 (3–5)	0.0 (—)
Western Kingbird	55	6.0 (5–7)	3.8 (3–6)	0.0 (—)
Scissor-tailed Flycatcher	16	6.5 (4–7)	3.5 (3–5)	0.0 (—)

[a]Starting points (primary number) for primary molts can be calculated as ten minus the number of feathers replaced.

[b]Note that one or more tertials can be replaced twice during the first year in kingbirds (see Table 2), but the totals for these species include each tertial once.

(*Pyrocephalus rubinus*), western Tropical Kingbird (*Tyrannus melancholicus occidentalis*; other subspecies were not examined for this study), Cassin's Kingbird (*T. vociferans*), Western Kingbird (*T. verticalis*), and Scissor-tailed Flycatcher (*T. forficatus*). Limited specimen evidence ($n = 4$) suggests that an eccentric replacement pattern also occurs in first-year Gray Kingbirds (*T. dominicensis*). Among other taxa of these genera, the Western (*Contopus sordidulus*; $n = 26$) and Eastern (*C. virens*; $n = 12$) wood-pewees, eastern Willow (*E. t. campestris/traillii*; $n = 6$) and Alder (*E. alnorum*; $n = 22$) flycatchers, and Eastern Kingbird (*T. tyrannus*; $n = 12$) replaced all remiges, whereas the Greater Pewee (*C. pertinax*; $n = 15$), the remaining *Empidonax* flycatchers (*virescens*, $n = 9$; *minimus*, $n = 18$; *hammondii*, $n = 28$; *oberholseri*, $n = 27$; *wrightii*, $n = 24$; *difficilis*, $n = 30$; *occidentalis*, $n = 16$; and *fulvifrons*, $n = 15$), and the Thick-billed Kingbird (*T. crassirostris*; $n = 16$) replaced no remiges or primary coverts, other than the tertials on some birds.

The eccentric replacement pattern is well illustrated in the Vermilion Flycatcher (Figure 1, Table 1). The number of remiges replaced ranged from all secondaries and primaries (in 53.7% of 82 first-year specimens examined, identified by the retention of juvenal primary coverts) to nine of 19 feathers (five outer primaries and four inner secondaries; CAS 39678). The number of outer primary coverts replaced varied from none (23.1%) to five (2.4%). In all cases, replacement proceeded consecutively from the starting points to the outermost primary and primary covert and to the innermost secondary other than the tertials. The sequence was confirmed with eight specimens collected during active molt. This pattern was also typical of first-year remex molts in the other flycatcher species showing the eccentric pattern, except for most Cassin's Kingbirds (see below). All replacement of remiges by Vermilion Flycatchers occurs in the late summer and fall; no spring replacement of flight feathers was found.

First-year Yellow-bellied and western Willow flycatchers differ from the Vermilion Flycatcher in that remex molt occurs during the spring rather than the fall (see also Dickey and van Rossem 1938, Mengel 1952, Johnson 1963); adults of these forms replace flight feathers in the fall (Johnson 1963, P. Unitt pers. comm.). First-year Olive-sided Flycatchers appear to have one protracted over-winter molt of flight feathers, commencing in September or October and concluding in March or April, although this needs confirmation as only three specimens I examined were collected on the winter grounds. Among first-spring Olive-sided Flycatcher specimens, 21.4% of 28 had replaced all remiges.

In the kingbirds, remex molt begins in the fall, is suspended over winter, and resumes in the spring (Table 2). The outer primary molt begins with one of P4, P5, or P6 (P7 in one Scissor-tailed Flycatcher), and the inner secondary molt (excluding the tertials, which typically molt before other secondaries) with one of S4, S5, or S6 (see Figure 1 for remex numbering). No specimens collected in winter (November through February; see Table 2) were in active molt, confirming that remex replacement occurs in stages rather than continuously through the winter. Cassin's Kingbird differs from the other three species in that fewer remiges are replaced during the first year (Table 1), including no primaries or secondaries (except tertials) in 36%

Table 2 Numbers (Mean and Range) of Remiges Replaced During the First Fall and Spring Molts in Four Species of Kingbirds

	First fall molt[a]			First spring molt[b]		
Species	*n*	Outer primaries	Inner secondaries	*n*	Outer primaries	Inner secondaries
Tropical Kingbird	12	2.3 (1–5)	4.0 (3–6)	13	3.2 (2–4)	5.4 (4–7)
Cassin's Kingbird	16	0.3 (0–1)	1.2 (0–3)	13	1.5 (0–5)	3.5 (3–5)
Western Kingbird	27	1.6 (0–3)	2.9 (1–4)	45	4.9 (3–6)	3.5 (3–6)
Scissor-tailed Flycatcher	21	1.9 (0–5)	3.0 (1–5)	13	4.7 (2–6)	3.1 (2–6)

[a]Based on specimens collected from November through February. Number of secondaries replaced during the fall molt includes the tertials, which are often replaced again during the spring molt (see text). Compare with the data presented in Table 1.

[b]Based on specimens collected from April through July.

of 14 specimens, and that the molt is usually (in 77% of the nine specimens showing replacement of primaries) arrested before the outermost primaries are replaced. Thus, many first-spring Cassin's Kingbirds had replaced, e.g., only P6–P7 and S6 (CAS 46202) or P5–P7 and S5–S6 (MVZ 4299).

The evidence indicates that the replacement of primaries in spring continues where the fall molt is suspended. Numerous spring and summer kingbirds show three generations of primaries, with the number and sequence of first-fall feathers (e.g. P5–P7 or P6–P7) being typical of fall replacement patterns shown by mid-winter birds. Among 27 Western Kingbirds collected in their first winter, for example, the mean number of primaries replaced during fall molts was 1.603 (± 0.907 [standard deviation]), whereas the mean number of first-fall primaries detected on 45 spring and summer birds was 1.589 (± 0.920). These similar figures (ANOVA, P = 0.824) support the premise that no primaries replaced during the fall molt are replaced again during the spring molt.

Among the secondaries, however, the tertials appeared to be replaced during the fall molt and again during the spring molt (see Table 2). Among Western Kingbirds, only six of 45 spring and summer birds (mean 0.155 ± 0.424) had retained one or two first-fall tertials, whereas 27 winter birds had replaced a mean of 2.885 (± 0.824) juvenal tertials. This highly significant difference (ANOVA, $P < 0.0001$) in the number of first-fall tertials present in winter versus spring indicates that the tertials typically replaced in the fall are replaced again in the spring. The other three species of kingbirds show similar patterns of fall and spring replacement of remiges (Table 2).

DISCUSSION

In several respects eccentric replacement patterns in tyrannid flycatchers differ from those documented in other North American passerines. The highly variable commencement points of this molt in the Vermilion and other flycatchers, the suspended eccentric pattern of the kingbirds, and the suspended and arrested eccentric pattern of most Cassin's Kingbirds are strategies that have rarely been documented, even in Europe (Jenni and Winkler 1994).

It has been suggested that eccentric molts occur in species that are more exposed to bright sunlight or that suffer higher feather wear due to harsh vegetation, the renewal of outer primaries and inner secondaries being needed for protection of underlying feathers and improved flight (Dwight 1900, Mester and Prünte 1982, Jenni and Winkler 1994). Willoughby (1991) suggested that vegetation might be more important than exposure to sunlight in the extent of first-year molts of *Spizella* sparrows. Many North American species that have eccentric primary molts, including the Verdin (*Auriparus flaviceps*), White-eyed Vireo (*Vireo griseus*), Yellow-breasted Chat, Field Sparrow (*Spizella pusilla*), *Passerina* buntings, and several species of wrens, thrashers, sparrows, and orioles (Willoughby 1991, Thompson and Leu 1994, Pyle 1997), reside in harsh vegetation. The occurrence of eccentric primary molting patterns in other species such as the tyrannid flycatchers, Loggerhead Shrike, Lark Bunting (*Calamospiza melanocorys*), and House Finch (*Carpodacus mexicanus*), extensively exposed to sunlight but not to harsh vegetation, suggests that exposure to sunlight may also affect the occurrence of these molts. In addition, variation within tyrannid genera suggests a correlation between length of migration and the extent of remex molts, those taxa that winter in South America generally replacing their remiges completely, those wintering in Central America largely showing eccentric patterns, and those wintering in Mexico or the United States molting fewer remiges on average. This corresponds, in general, with patterns found in European migrants (Jenni and Winkler 1994), although it differs from what is found among *Passerina* buntings, where both migratory and resident species molt to a similar extent (Thompson 1991, Young 1991, Thompson and Leu 1995). Migration distance, as well as vegetation, exposure to sunlight, and other factors, should thus be considered when causes and extents of eccentric molts are addressed.

Clearly, more study is needed on eccentric molts in North American passerines, their causes, and to what extent these molts in different genera represent homologous patterns.

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