

MOLT STRATEGIES BY AGE AND SUBSPECIES IN THE WILLOW FLYCATCHER

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ABSTRACT: We clarify the molt strategies of the Willow Flycatcher (*Empidonax traillii*) by subspecies through the examination of 455 museum specimens. Most and typically all juvenile primary coverts are retained during the preformative molt in fall and winter, allowing yearlings to be distinguished from older birds from their first spring through their second fall. In addition to replacing the body feathers and some to (usually) all secondary coverts and tertials, the preformative molt can include no other remiges or rectrices (46% of specimens), all remiges and rectrices (33%), or some remiges in an “eccentric” sequence (21%). During the prealternate molt, replacement of upper wing coverts and tertials is much less extensive than in the preformative molt, varying from replacement of no feathers in 27% of specimens to replacing more than half of the median and greater coverts and all three tertials in other specimens. Both the preformative and the first prealternate molts are significantly more extensive in eastern *E. t. traillii* than in the three western subspecies (*brewsteri*, *adastus*, and *extimus*). The definitive prealternate molt is also significantly more extensive than the first prealternate molt in the western subspecies but not in *traillii*. These differences between *traillii* and the other subspecies may result from longer migration distances, hence more solar exposure on an annual basis, and different molt-strategy dynamics between eastern and western North American passerines, perhaps relating to preferences for moister habitats. Further investigation is needed on the timing of molts on the winter grounds and the extent of body-feather replacement during the prealternate molt.

Determination of a bird’s age or cohort is critical for studies of avian demography, distributional patterns, behavior, and the conservation of declining species. For example, Pyle et al. (2020) found that the ratio of yearlings to older individuals among boreal forest birds indicated the older birds exclude yearlings from preferred breeding habitats through despotism, a dynamic that could inform habitat management. Understanding molt strategies is, in turn, critical to age determination, but for many North American species that molt away from their breeding grounds, these strategies are poorly known (Pyle 1997a, 2022a, Pyle et al. 2009, 2018a, 2022). Fitness consequences and factors driving the evolution of molt, such as migration distance and habitats, have also been understudied because of lack of detailed information for most species and differing opinions on the definition of molts that occur away from breeding grounds (Pyle 2022a).

The Willow Flycatcher (*Empidonax traillii*) breeds widely across the United States and winters over a broad latitudinal range, from west-central Mexico to northern South America (Sedgwick 2020). Currently, four subspecies are recognized (following Clements et al. 2021; see also Unitt 1987, Browning 1993): *E. t. traillii* (*campestris* being a synonym), which breeds east of the Rocky Mountains and winters to South America; *E. t. brewsteri*, which breeds west of the Sierra Nevada and Cascade ranges and winters primarily in western Mexico and Central America; *E. t. adastus*, which breeds between the Cascade/Sierra Nevada and Rocky Mountain ranges and winters primarily

in Central America; and *E. t. extimus*, which breeds or formerly bred in the southwestern United States from southern California to New Mexico and winters in western Central America (Kelly et al. 2008, Ruegg et al. 2021). Many populations of the Willow Flycatcher are declining (Whitfield and Sogge 1999, Sedgwick 2020, Loffland et al. 2022), and the U.S. Fish and Wildlife Service has designated *E. t. extimus* as endangered (Unitt 1987, USFWS 1995, Ruegg et al. 2018, 2021).

The Willow Flycatcher's molt patterns and age-determination criteria were last summarized by Pyle (1997a:224–228), who stated that all molts occur on the winter grounds, that the sequences and extents of the molts were not known, and that the molt strategies of various populations of the Willow Flycatcher may differ from each other and from those of the very similar Alder Flycatcher (*E. alnorum*). Clearly, more study based on individuals of known species, subspecies, and age is needed. As age-determination criteria in the Willow Flycatcher are based entirely on molt patterns, the incomplete knowledge of the species' molt strategies has hampered our ability to distinguish yearlings from older individuals (Pyle 1997a).

Carnes et al. (2021) clarified the molt strategies of the Alder, Least (*E. minimus*), and Yellow-bellied (*E. flaviventris*) flycatchers, species of *Empidonax* that also molt primarily on their winter grounds. That study confirmed that the Alder Flycatcher typically retains all juvenile primary coverts through the preformative and first prealternate molts, allowing yearlings to be distinguished from older individuals in spring and summer (Carnes et al. 2021). We thus hypothesize that the Willow Flycatcher may exemplify the same pattern.

Improved knowledge of molt strategies and their subspecific differences should improve age-determination criteria for the Willow Flycatcher and may assist with subspecific identification in the field, especially for birds on migration and the winter grounds. Detailed study based on consistent interpretation of molts away from breeding grounds should also help us understand factors driving the evolution of these molts. If, as in other species of *Empidonax* (Pyle et al. 2020), older Willow Flycatchers also exclude yearlings from their preferred habitats, improved knowledge of the species' molts, age-determination criteria, and subspecies identification will assist in its conservation.

We reevaluated the Willow Flycatcher's molt strategies in light of new information on other species of *Empidonax* that molt in their winter range, focusing on potential differences among the four subspecies. Our methods and interpretation of molt and plumage terminology follow those of Carnes et al. (2021), although our data are from museum specimens rather than captured live birds.

METHODS

Pyle examined all specimens of the Willow Flycatcher located at the California Academy of Sciences (CAS), San Francisco, and the Museum of Vertebrate Zoology (MVZ), Berkeley. Each specimen was carefully identified to species (ensuring exclusion of the Alder Flycatcher) and subspecies by the criteria of Unitt (1987) and Pyle (1997a) and with the aid of information on the specimen labels and direct comparison among series of each subspecies.

Although the plumage of these subspecies is similar (Paxton et al. 2010, Mahoney et al. 2020), with extensive series available, with a conservative approach regarding many specimens, and accounting for the effects of plumage wear (see Results), we believe that our subspecific identifications are adequate for this analysis, especially regarding *E. t. traillii*, which differs from the western subspecies in wing structure as well as coloration of body plumage and wing-feather edging (Unitt 1987, Pyle 1997a, Paxton et al. 2010). We also examined images at the Cornell Lab of Ornithology's Macaulay Library for both subspecies differences and molt patterns; the Macaulay Library catalog has become a valuable complement to specimens for studies of molt (cf. Pyle 2022b).

Following Pyle (1997a) and with criteria confirmed during this study (see below), we categorized each individual to molt cycle (age) and plumage according to the “WRP” system (Wolfe et al. 2010, Pyle et al. 2022). Plumage categories included juvenile (FCJ), formative (FCF), first alternate (FCA), definitive basic (DCB), and definitive alternate (DCA). A few specimens were collected while undergoing active preformative or prebasic molt; we excluded these birds from our analyses as the ultimate extent of their molt could not be known. None of the examined specimens was undergoing a prealternate molt insofar as we could detect. Molt terminology follows that of Carnes et al. (2021) who, contra Pyle (1997a), considered most wing-feather replacement on winter grounds to result from suspended and protracted preformative and prebasic molts, which can be completed in spring and overlap more limited prealternate molts (see also Pyle 2022a).

For each specimen in formative or alternate plumage, we analyzed feather-replacement patterns by age and plumage class, with the goal of describing the extent and sequence of replacement during preformative and prealternate molts. Feathers within alar tracts of one wing were scored for the 9 median coverts, the 11 greater coverts (including the carpal covert), the 3 alula feathers, the 3 tertials, the 6 remaining secondaries, the 10 primaries, and the outer 5 (of 10) primary coverts; up to 5 inner primary coverts could not be examined without damaging specimens. We attempted to score lesser coverts by the methods of Guallar and Jovani (2019) but did not trust our accuracy on specimens and thus omitted this tract from analyses. A composite score for the overall extent of each molt thus ranged from 0 (no feathers replaced) to 47 (all of the above feathers replaced). We examined both wings of all specimens to ensure that replacement was due to symmetrical molt rather than adventitious replacement.

For birds in formative plumage, we categorized each feather as juvenile or formative; for birds in first alternate plumage, we categorized each feather as juvenile, formative, or first alternate; and for birds in definitive alternate plumage, we categorized each feather as basic or alternate. We identified feather generations on the basis of plumage color, degree of feather wear, contrasts between retained and replaced feathers (molt limits), and feather position (see Figure 1). We assumed that replacement of coverts during the preformative molt was proximal to distal within each tract and that the tertials were replaced in the sequence s8–s9–s7, as in most passerines (Pyle 1997a, 2022a, Jenni and Winkler 2020). Alternate feathers located earlier in the above sequence and within a group of otherwise formative feathers (e.g.,

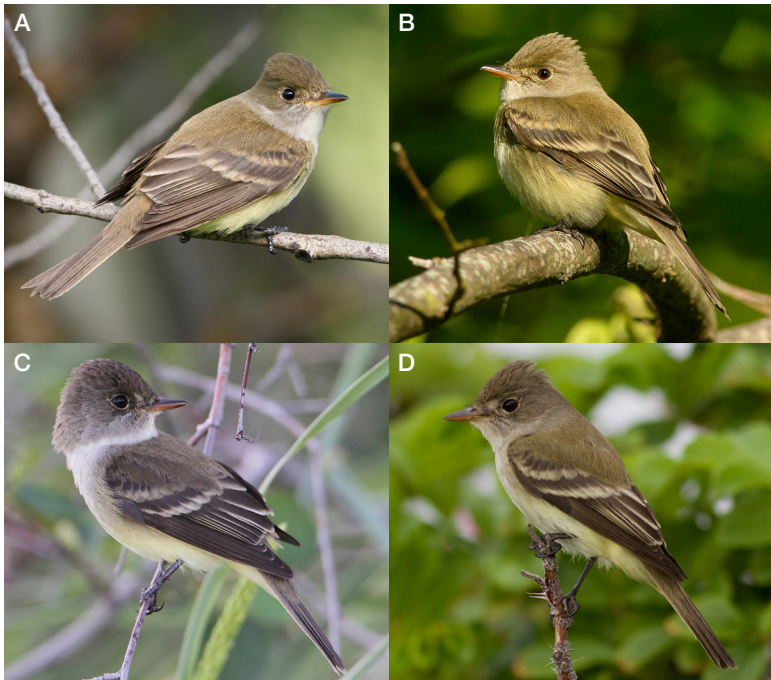


FIGURE 1. Willow Flycatchers in first alternate (A, B) and definitive alternate (C, D) plumages. In the birds in first alternate plumage, the juvenile primary coverts have been retained and are worn and brown, contrasting with the replaced greater coverts. A, the outer greater coverts and s8–9 appear formative, the inner three median and greater coverts appear to be first alternate, and the remaining remiges and rectrices appear juvenile. B, most wing feathers appear to be formative, although it is possible that some juvenile inner primaries or outer secondaries have been retained in an eccentric sequence. The inner six median coverts, inner four greater coverts, and inner two tertials (s8–9) appear to be first alternate feathers. In the birds in definitive alternate plumage, note the black basic primary coverts, in contrast to the retained grayish juvenile coverts in A and B. C, no wing coverts have been replaced, but s9 appears to be alternate. D, the inner four median coverts and five greater coverts along with all three tertials (s7–s9) appear to be alternate. A and C, *E. t. adastus*, which averages fewer feathers replaced during the preformative and prealternate molts. B and D, *E. t. traillii*, which averages more feathers replaced during these molts. Photos cropped and used by license agreement from the Macaulay Library. Photos by Darren Clark (A; ML245017611, Idaho, 18 June 2020), Daniel Irons (B; ML58268541, Maryland, 15 May 2017); Marlene Cashen (C; ML240956261, Washington, 3 June 2020), and Nathan Dubrow (D; ML347139971, Maine, 11 June 2021).

inner greater coverts, s8) we assumed also to have been replaced during the previous preformative molt (see Figures 1, 2).

Following Pyle (1997a), we numbered the primaries from the innermost (p1) to outermost (p10) and the secondaries from the outermost (s1) to innermost (s9), including the three tertials (s7–s9). For first-year birds, we also

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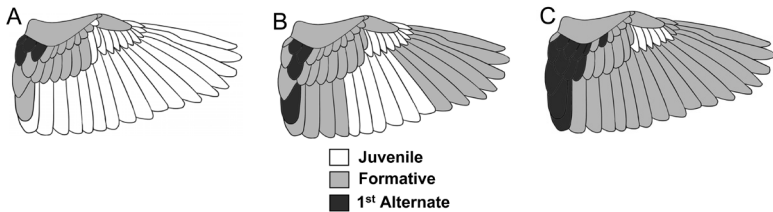


FIGURE 2. Variation in the extent of the preformative and prealternate molts of the Willow Flycatcher; note that molt of the lesser coverts was not evaluated. The preformative molt can vary from partial (A) to incomplete with an eccentric pattern (B) to almost complete (C), although most to all primary coverts are retained juvenile feathers, allowing birds to be aged in spring and summer. The preformative molt is always more extensive than the first prealternate molt, allowing assessment of the extent of both molts on birds collected in spring; on the basis of documented replacement sequences, these first alternate feathers were presumably also replaced during the preformative molt (see Pyle 2022a and text). Illustrations based on specimens MVZ 111161 (A; *E. t. brewsteri*), CAS 3186 (B; *E. t. extimus*), and MVZ 168698 (C; *E. t. traillii*).

scored rectrices as uniformly juvenile, uniformly formative, or a mixture of the two generations; we observed no rectrices grown during the prealternate molt.

We analyzed the extent of preformative, first prealternate, and definitive prealternate molts with generalized linear models implemented through the open-source program R (R Core Team 2021). The model of each episode of molt contained subspecies as a fixed effect. Feather-count data were modeled as a Poisson distribution. For birds in first alternate plumage, we used Spearman rank correlations to determine whether the extents of the preformative and first prealternate molts were correlated at both the species and subspecies levels. We also used Spearman rank correlations to compare the extent of replacement between feather tracts by molt episode to see if the extents in these tracts were correlated.

RESULTS

The 455 specimens of the Willow Flycatcher for which we scored for molt included 32 of *E. t. traillii*, 139 of *E. t. adastus*, 239 of *E. t. brewsteri*, and 23 of *E. t. extimus*. The remaining 22 specimens were not confidently placed to subspecies because of intermediacy, perhaps indicating intergradation, or worn plumage that precluded accurate evaluation; these were primarily between *adastus* and *brewsteri* (20 specimens) with one specimen between *adastus* and *extimus* and one between *adastus* and *traillii*. Specimens unidentified to subspecies were included in species-level but not subspecies-level analyses. Subspecific identifications agreed with those on specimen labels for the majority of specimens, but we reidentified the subspecies of 24 specimens and added subspecific designations to 159 otherwise unlabeled specimens.

During the course of this study, we confirmed that molt of wing feathers takes place on winter grounds and that most or all first-year birds retain their juvenile primary coverts until their second prebasic molt, allowing yearlings

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and adults to be distinguished in spring and summer (Figures 1, 2). As in the Alder Flycatcher (Carnes et al. 2021), we also confirmed that replacement of primaries, secondaries, and rectrices during the preformative molt varies from none to complete.

On the basis of these criteria, we categorized specimens to age and molt status as follows: juvenile plumage, 96 specimens; formative plumage, 1; first alternate plumage, 101; definitive basic plumage, 2; definitive alternate plumage, 247; undergoing active preformative molt when collected, 4; undergoing second prebasic molt, 2; undergoing second or later prebasic molt, 1. The paucity of specimens in formative or basic plumage or in active molt reflects bias, in the two collections studied, toward specimens collected away from the winter grounds where most to all molt and the formative and basic plumages occur. Our sample sizes for analyzing the extent and sequence of molt were 102 for the preformative molt (formative and first alternate plumages pooled), 101 for the first prealternate molt (first alternate plumage only), and 247 for the definitive prealternate molt. After exclusion of 14 specimens not identified to subspecies, these included 26 specimens of *E. t. traillii*, 119 of *E. t. adastus*, 172 of *E. t. brewsteri*, and 18 of *E. t. extimus* (Table 1).

All 96 birds with wing feathers entirely juvenile were collected in Canada or the United States on dates ranging from 25 July (MVZ 3182, *extimus*) to 11 October (MVZ 27225, *brewsteri*). We examined these specimens' alar tracts

TABLE 1 Mean Number of Selected Upperwing Coverts and Remiges Replaced during the Preformative, First Prealternate, and Definitive Prealternate Molts of the Willow Flycatcher by Subspecies^a

Subspecies and molt	Median coverts	Greater coverts	Tertials	Secondaries	Primaries	Total
All						
Preformative	9.88	9.30	2.67	2.94	4.90	32.33 ± 9.80
First prealternate	<i>1.57</i>	<i>1.32</i>	<i>0.96</i>	0.00	0.00	3.85 ± 4.03
Definitive prealternate	<i>2.10</i>	<i>1.87</i>	<i>1.42</i>	0.00	0.00	5.38 ± 4.16
<i>E. t. traillii</i>						
Preformative	10.00	10.00	2.91	5.00	8.73	40.55 ± 5.84
First prealternate	3.18	3.09	2.18	0.00	0.00	8.45 ± 3.70
Definitive prealternate	2.33	2.40	1.87	0.00	0.00	6.60 ± 3.89
<i>E. t. brewsteri</i>						
Preformative	9.89	9.38	2.70	2.80	4.68	31.96 ± 9.20
First prealternate	1.49	1.16	1.05	0.00	0.00	3.42 ± 3.79
Definitive prealternate	<i>1.98</i>	<i>1.84</i>	<i>1.27</i>	0.00	0.00	5.09 ± 4.15
<i>E. t. adastus</i>						
Preformative	9.75	8.71	2.50	2.46	4.08	29.96 ± 11.37
First prealternate	1.33	1.25	1.04	0.00	0.00	3.63 ± 3.74
Definitive prealternate	<i>2.14</i>	<i>1.78</i>	<i>1.45</i>	0.00	0.00	5.37 ± 4.33
<i>E. t. extimus</i>						
Preformative	10.00	9.38	2.50	2.13	3.00	29.25 ± 8.75
First prealternate	1.25	0.88	0.88	0.00	0.00	3.00 ± 3.42
Definitive prealternate	<i>2.20</i>	<i>2.10</i>	<i>1.70</i>	0.00	0.00	6.00 ± 3.86

^aSee text for sample sizes. Not shown are alula feathers and primary coverts (see text), which are calculated in the total for each molt. Bold font denotes significant differences between subspecies; italics denote significant differences in extent of molt between plumage classes.

closely for indication of molt on summer grounds and detected no feathers representing the formative plumage. However, one specimen collected in Oregon on the unusually late date of 18 October 1981 (MVZ 169102, *brewsteri*) was undergoing preformative molt and had replaced all median coverts, six inner greater coverts, s8, s9, and r1. Otherwise, it appears that Willow Flycatchers do not begin molting their wing feathers until they reach their winter grounds. Preformative molt of body feathers before migration has been reported in the Willow Flycatcher (Hussell 1991) and other *Empidonax* flycatchers (Carnes et al. 2021); we did not detect any body-feather replacement in these 96 specimens, although limited replacement of body feathers can be hard to detect and may have been missed.

The remaining three birds undergoing preformative molt of wing feathers were collected in Mexico and South America between 27 September (MVZ 154585, *trillii*) and 18 November (MVZ 163861, *trillii/adastus*). The three birds collected while undergoing prebasic molt were two in second prebasic molt, MVZ 93895 (*trillii*, replacing p5 on 29 January) and MVZ 86027 (*brewsteri*, replacing p3 on 24 February), and one in second or later prebasic molt, CAS 32698 (*brewsteri*, completing growth of p9 and p10 on 25 November). The three birds undergoing preformative molt were not replacing primary coverts with corresponding primaries, whereas the three birds undergoing prebasic molt were replacing these corresponding feathers synchronously.

All 101 specimens in first alternate plumage had retained some formative wing coverts and/or tertials/secondaries, so the preformative molt was more extensive than the first prealternate molt in all cases (Table 1, Figures 2, 3). In these, first alternate wing feathers were confined to inner median and greater coverts and inner two tertials, and we assumed these feathers had also been replaced during the preformative molt (cf. Figure 2). Among these specimens, plus the one in formative plumage, the preformative molt varied from partial, involving only four inner greater coverts and seven inner median coverts (MVZ 184838, *adastus*; composite score 11; see also Figure 2A) to nearly complete, involving all secondary coverts, secondaries, and primaries, and the outer five primary coverts replaced (MVZ 73560, *adastus*, and MVZ 168702, *trillii*; composite score 46; see also Figure 2C). All juvenile primary coverts had been retained in 95 of 102 specimens (93%). In 47 specimens (46%) no primaries had been replaced, whereas in 34 (33%), all primaries were replaced. The remaining 21 specimens (21%) had molted in an “eccentric” pattern, in which the outer primaries and inner secondaries were replaced but the juvenile inner primaries and outer secondaries were retained (Figure 2B; see Pyle 1998). The number of juvenile feathers retained during eccentric molt varied from one (p1 only; CAS 76446, *extimus*) to seven (p1–p4 and s1–s3; MVZ 33374, *brewsteri*). In all cases of partial molt of the secondary coverts, consecutive inner greater and median coverts were replaced while consecutive outer coverts were retained, i.e., no feathers were skipped or replaced out of sequence. Tertials but not other secondaries were replaced in 38 specimens (37%), the number replaced ranging from 1 (3 specimens) to all 3 tertials (22 specimens). When 1 tertial was replaced it was always s8, and when 2 were replaced they were always s8 and s9.

Poisson regression showed that the preformative molt was significantly more extensive in *E. t. trillii* than in the other three subspecies ($Z = 78.190$,

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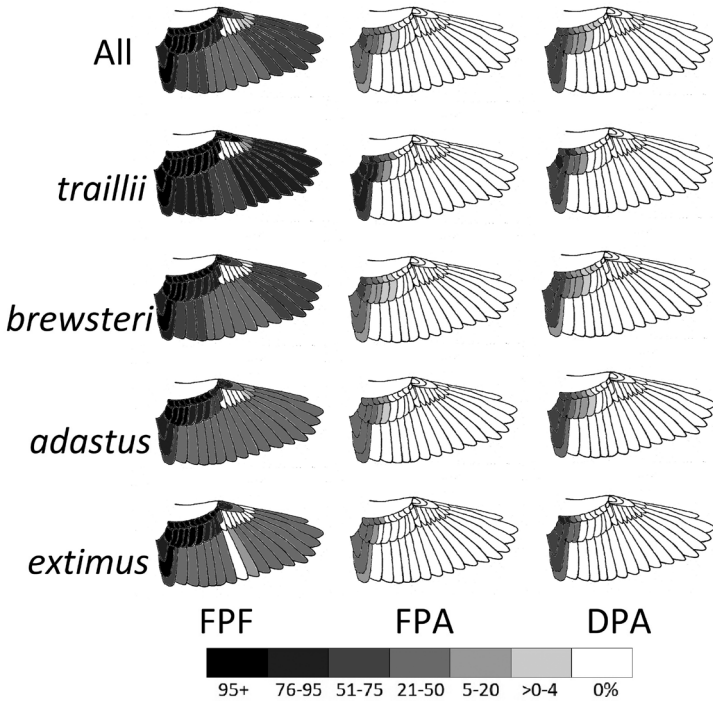


FIGURE 3. Frequency of replacement of the median coverts, greater coverts, and remiges during the preformative (FPF), first prealternate (FPA), and definitive prealternate (DPA) molts of the Willow Flycatcher, overall and by subspecies. Shades of gray represent frequency of observed replacement (lesser coverts not scored). See text for sample sizes for each subspecies and molt.

$P < 0.001$) whereas the other three subspecies did not differ in extent of molt (Table 1, Figure 3). For example, replacement of primaries was found in 91% of 11 *traillii*, 54% of 56 *brewsteri*, 42% of 24 *adastus*, and 38% of 8 *extimus*. The mean number of primaries replaced in *traillii* also differed from that in the other three subspecies ($Z = 21.227$, $P < 0.001$; Table 1). The percentage of specimens undergoing an eccentric preformative molt was higher in *extimus* (38%) and *brewsteri* (24%) than in *traillii* (18%) and *adastus* (8%). Rectrices were fully replaced during the preformative molt in all specimens that had replaced primaries. Among 47 specimens with no primaries replaced, 22 had replaced no rectrices, 23 had replaced all rectrices, and only two had mixed formative and juvenile rectrices, in both cases having replaced the central but no other rectrices.

On the basis of 358 specimens in alternate plumage (first alternate and definitive alternate combined), the prealternate molt was much less extensive than the preformative molt (Table 1, Figure 2): composite molt scores were 32.33 for the preformative molt, 3.85 for the first prealternate molt, and 5.38

for the definitive prealternate molt. The prealternate molt did not include any wing feathers in 97 specimens (27%), including 39% of those in first alternate plumage and 24% of those in definitive alternate plumage. Replacement of wing coverts among the remaining 251 specimens varied from only one median covert (5 specimens) or only one greater covert (4 specimens) replaced to 8 inner median coverts and 5 inner greater coverts replaced (CAS 35351, *brewsteri*, in definitive alternate plumage). Replacement usually involved consecutive inner coverts, although in 14 specimens (5.6% of those replacing coverts) one or more inner median coverts were retained within a series of replaced coverts, and in 19 specimens (7.6%) the same was true within a series of replaced greater coverts (cf. Figure 2C). From one (36 specimens) to all three (70 specimens) tertials were replaced in 205 specimens (57%; 47% of those in first alternate plumage and 62% of those in definitive alternate plumage). When one tertial was replaced, it was s8 in 22 specimens and s9 in 14 specimens; when two were replaced it was always s8 and s9.

Poisson regression showed that the definitive prealternate molt was significantly more extensive than the first prealternate molt at the species level ($Z = -5.8$, $P < 0.001$), and in all subspecies but *traillii*, in which the extent of the first prealternate molt was nearly significantly greater than that of the definitive prealternate molt ($Z = 1.72$, $P = 0.086$). The first prealternate molt was significantly more extensive in *E. t. traillii* than in the other three subspecies (*traillii* composite score 8.45, others composite scores 3.00–3.63, $Z = 20.9$, $P = < 0.001$), whereas its extent among the other three subspecies did not differ (Table 1, Figure 2). The definitive prealternate molt was more extensive in *traillii* (composite score 6.60) than in *brewsteri* (composite score 5.09; $Z = 18.8$, $P < 0.001$), but otherwise its extent was similar among the four subspecies (Tables 1, 2, Figure 1).

Spearman rank correlations indicated a positive relationship between the extent of the preformative molt and that of the first prealternate molt ($r_s = 0.43$, $P < 0.001$). In other words, individuals in which the preformative molt was more extensive tended to have the first prealternate molt more extensive as well. By subspecies, this trend was significant in *brewsteri* ($r_s = 0.37$, $P = 0.005$) and nearly significant in *traillii* ($r_s = 0.56$, $P = 0.07$) but not significant in *adastus* or *extimus*.

Within all three molts, the extent of replacement of the median coverts and greater coverts and the extent of replacement of the greater coverts and tertials were highly correlated (Figures 4, 5). Additionally, extents of replacement of the secondaries and primaries during the preformative molt were highly correlated ($r_s = 0.94$, $P < 0.001$), as was replacement of primary coverts with that of the primaries ($r_s = 0.34$, $P < 0.001$). Therefore, in all cases, a greater number of feathers replaced in one tract was strongly correlated with a greater number replaced in other tracts.

DISCUSSION

We have confirmed that most or (usually) all juvenile primary coverts are retained during the preformative molt of the Willow Flycatcher (Figure 2). As in the Alder Flycatcher (Carnes et al. 2021), this allows yearlings to be distinguished confidently from older birds the following spring. A pat-

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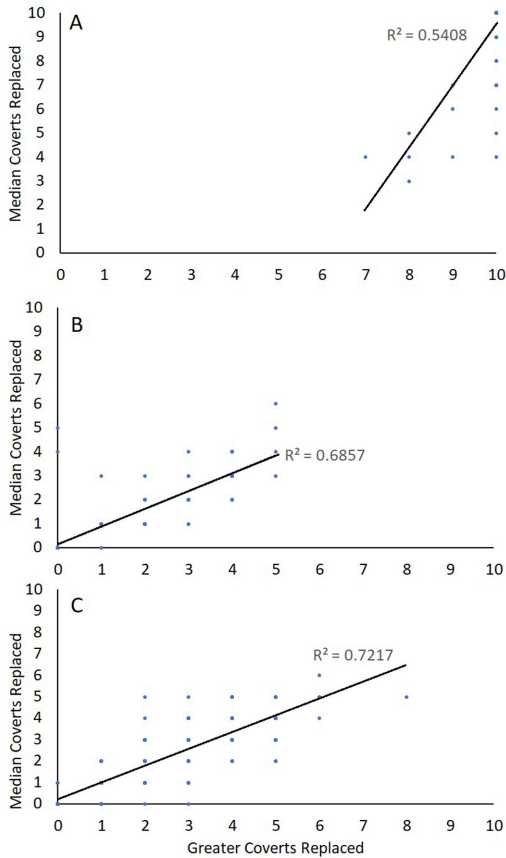


FIGURE 4. Correlations between extent of replacement of median coverts replaced with numbers of greater coverts replaced during preformative (A), first prealternate (B), and definitive prealternate (C) molt in the Willow Flycatcher. For all three molts the correlation was significant ($r_s > 0.54$, $P < 0.001$).

tern of some to all primaries but fewer primary coverts being replaced has been found in other species of North American flycatchers and other birds, especially in those in which primaries and secondaries may be replaced in the eccentric pattern (Pyle 1997a, 1998, Burton and Pyle 2006). Although there is little evidence of the prebasic molt of passerines falling short of complete, S. Guallar (pers. comm.) has suggested that a small proportion of some tyrannid flycatcher species may retain a few inner primary coverts during otherwise complete prebasic molts, as known in woodpeckers (Pyle 1997a). Further investigation is needed to determine whether this pattern (shown by 7% of the birds that we assumed reflected preformative molt) can result from an incomplete prebasic molt. In any case, with improved ability to age Willow

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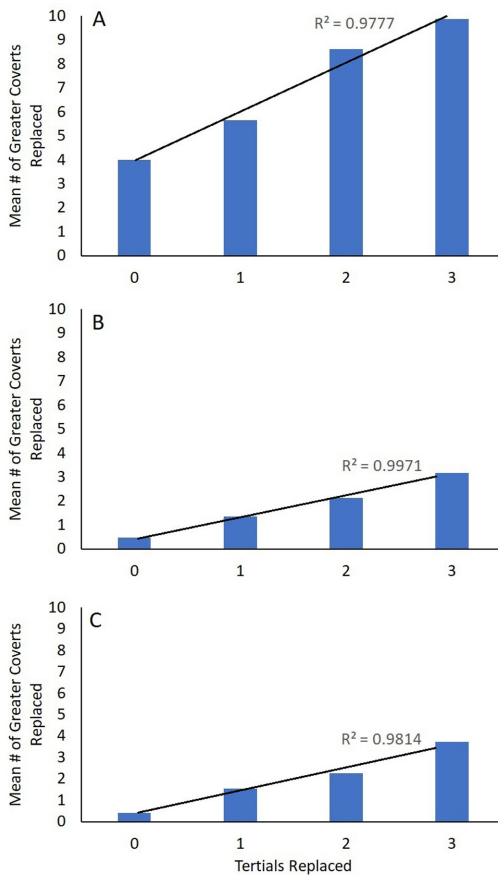


FIGURE 5. Mean number of greater coverts replaced when 0, 1, 2, or 3 tertials were replaced during preformative (A), first prealternate (B), and definitive prealternate (C) molt in the Willow Flycatcher. For all three molts the correlation was significant ($r_s > 0.54$, $P < 0.001$).

Flycatchers on the breeding grounds, we look forward to establishment of more informed conservation metrics for the declining populations in western North America (cf. Loffland et al. 2022). For example, we can now investigate whether or not yearling Willow Flycatchers may be excluded from optimal habitats by older birds, leading to more directed management of optimal habitats in which older birds breed (cf. Pyle et al. 2020).

We found the preformative and prealternate molts of *E. t. traillii* to be significantly more extensive than in the three western subspecies of the Willow Flycatcher. This difference fits an overall pattern of flycatchers and other birds wintering at more southerly latitudes undergoing more extensive molts (Pyle 1998, Carnes et al. 2021), possibly related to increased solar exposure

on an annual basis resulting in increased wear and need for more frequent feather replacement (Pyle 1998, 2008, Terrill et al. 2020, Guallar et al. 2021). A higher proportion of eccentric molt, as in the western subspecies of the Willow Flycatcher, is also expected of species or subspecies inhabiting drier environments (Willoughby 1991, Pyle 1997b, 1998). Increased solar exposure and/or effects of harsher habitat may have promoted the occurrence of this molt pattern, whereas reduced resources in such habitats may have prevented more complete molt of remiges, as found in some species inhabiting moister habitats. Consistent with this, among a sample of 82 Alder Flycatchers, a long-distance migrant of boreal northern and eastern North America, none were found with eccentric patterns of preformative molt (Carnes et al. 2021). Hence an eccentric preformative molt appears to be a criterion distinguishing some Willow Flycatchers in formative and first alternate plumages from the Alder Flycatcher. However, virtually the full range of extents and patterns of molt occurs among all four subspecies of the Willow Flycatcher, precluding the use of extent of molt in the identification of subspecies.

We found that individual Willow Flycatchers with a more extensive preformative molt also underwent a more extensive first prealternate molt, and that, at the species level, the definitive prealternate molt is more extensive than the first prealternate molt. These results differ from those of other *Empidonax* flycatchers. For example, there is a negative correlation between the extents of the preformative and prealternate molts in individual Yellow-bellied Flycatchers, and the first prealternate molt is more extensive than the definitive prealternate molt in the Alder and Least flycatchers (Carnes et al. 2021). When we compared extent of prealternate molt within each subspecies, however, we found that the definitive prealternate molt was more extensive than the first prealternate molt in *E. t. traillii*, opposite to that of the other three subspecies and more consistent with that in Alder and Least flycatchers.

Migratory passerines breeding in eastern and western North America tend to differ in molt strategy (Rohwer et al. 2005, Pyle et al. 2018a, Pageau et al. 2020), even within species such as the Warbling Vireo (*Vireo gilvus*), Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), Gray Catbird (*Dumetella carolinensis*), and Chipping Sparrow (*Spizella passerina*) (Yuri and Rohwer 1997, Voelker and Rohwer 1998, Pyle et al. 2018a). These differences appear to result from environmental factors related to summer being drier in the west than in the east, the same factors that result in molt-migration being longer for western than for eastern species and populations (Rohwer et al. 2005, Pyle et al. 2018a). We propose that these geographic differences along with differences in wintering habitats, as proposed for other *Empidonax* flycatchers (Carnes et al. 2021), may explain our subspecies-level results for the Willow Flycatcher.

Correlations between preformative and first prealternate molts have not been reported frequently, in part because of differing opinions on the definition of these molts (cf. Guallar and Figuerola 2016, Pyle 2022a), but the positive correlation we found in the Willow Flycatcher could relate to individuals' fitness, the fitter birds undergoing more extensive molts in both cases. Likewise, more extensive definitive prealternate than first prealternate molt in the western subspecies could result from older birds being fitter and/or more experienced than first-year birds, enabling them to acquire

more resources to replace more feathers. The opposite pattern in *E. t. traillii* may, as in the Alder Flycatcher, reflect different molt strategies as affected by longer-distance migration and preference for wetter habitat in both summer and winter (Carnes et al. 2021). Possibly, migration distance may predominate over habitat considerations as a factor, as in eastern North America most resident species or short-distance migrants undergo partial molts (no remiges replaced), whereas congeners in the west undergo eccentric molts (Pyle 1997b).

We found strong correlations between the number of feathers replaced in one alar tract with those replaced in other alar tracts. This is not surprising given the known distributions of replaced feathers, for example, those resulting in molt limits between juvenile and formative feathers (Pyle 1997a, Jenni and Winkler 2020). Nevertheless, this correlation has rarely been verified statistically (see Gargallo 1997 for one example). We also found that the position of replacement appeared to be rather fixed among feathers within each tract, adjacent proximal median and greater coverts being replaced and adjacent distal feathers being retained, without gaps or skipped feathers. We found no exceptions to this pattern with the preformative molt, whereas prealternate molts occasionally diverge from this sequence, 6–7% of individuals showing gaps in the molt of coverts.

These patterns are consistent with a trend in passerines toward greater variability in prealternate than in preformative molt (Guallar and Jovani 2019) and support the conclusion that preformative molt is more fixed in sequence (or at least outcomes of replacement) than is prealternate molt. We suggest that variation in the extent of preformative molt may be related to the time constraints that molt imposes, resulting in correlated fixed sequences within each tract being arrested at the same time. The date of hatching appears to be a factor, birds hatching later having less time and undergoing less extensive preformative molts than do those hatching earlier (Bojarinova 1999, Elrod et al. 2011).

Prealternate molt, on the other hand, though based in part on a need to replace worn feathers, shows evidence that social and sexual signaling have affected the color and position of replaced feathers in this molt (Guallar and Jovani 2019, Terrill et al. 2020). In *Setophaga* warblers, for example, the prealternate molt of the median and greater coverts more frequently involves medial feathers within each tract while skipping proximal and distal feathers (Pyle unpubl. data). These central feathers are more exposed on the closed wing than are the proximal feathers, enhancing their value for social signaling. The sequence can vary more during prealternate molt than during preformative molt, possibly indicating that these molts differ in their underlying mechanisms, as has been suggested for ducks (Pyle 2013) and gulls (Pyle et al. 2018b). *Empidonax* flycatchers differ from *Setophaga* warblers in that the alternate plumages are similar to the formative and basic plumages. This difference may help explain the rather fixed outcomes of prealternate molt, favoring replacement of more exposed feathers rather than replacement for social signaling, although it may also be possible that individual flycatchers can detect the number of formative and/or alternate feathers replaced and use this as a measure of the fitness of potential mates (cf. Guallar and Figuerola 2016).

From our examination of birds collected largely on the summer grounds or during migration, we were unable to assess the timing of the Willow Flycatcher's replacement of wing and body feathers during each molt. One specimen of *E. t. trillii* and another of *brewsteri* undergoing second prebasic molt were replacing middle primaries in January and February, whereas one of *brewsteri* that was undergoing either the second or later molt was replacing the outermost primaries in November. This difference in the timing may reflect age, with the second prebasic molt occurring on average later in the spring, as has been reported in *Empidonax* for replacement of primaries during the preformative molt (Dickey and van Rossem 1938, Pyle 1997a, Carnes et al. 2021). Likewise, it is unknown how often or when body feathers are replaced on the winter grounds. For example, are there two complete replacements of body feathers or is replacement during the prealternate molt limited or partial? Further study of the timing of molts on the winter grounds and the extent of body-feather replacement during prealternate molt is needed.

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LITERATURE CITED

- Bojarinova, J. G., Lehtikoinen, E., and Eeva, T. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. *J. Avian Biol.* 30:437–446; <https://doi.org/10.2307/3677016>.
- Browning, M. R. 1993. Comments on the taxonomy of *Empidonax trillii* (Willow Flycatcher). *W. Birds* 24:241–257.
- Burton, K., and Pyle, P. 2006. Some unexpected primary-covert molt limits. *N. Am. Bird Bander* 31:121.
- Carnes, B. H., Godwin, C. M., Foster, K. R., and Pyle, P. 2021. Clarification of molt strategies in three *Empidonax* flycatchers. *Wilson J. Ornithol.* 133:34–42; <https://doi.org/10.1676/20-00109>.
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Sullivan, B. L., and Wood, C. L. 2021. The eBird/Clements checklist of birds of the world, version 2021; <https://www.birds.cornell.edu/clementschecklist/>.
- Dickey, D. R., and van Rossem, A. J. 1938. The birds of El Salvador. *Field Mus. Nat. Hist. Zool. Ser.* 23:1–609.
- Elrod, M. L., Seavy, N. E., Cormier, R. L., and Gardali, T. 2011. Incidence of eccentric molt in first-year Wrentits increases with fledge date. *J. Field Ornithol.* 82:325–332; <https://doi.org/10.1111/j.1557-9263.2011.00336.x>.
- Gargallo, G. 1997. Ageing Cetti's Warbler *Cettia cetti* by means of plumage characteristics. *Ringing & Migration* 18:14–17; <https://doi.org/10.1080/03078698.1997.9674134>.
- Guallar, S., and Figuerola, J. 2016 Factors influencing the evolution of moult in the

- nonbreeding season: Insights from the family Motacillidae. *Biol. J. Linnean Soc.* 118:774–785; <https://doi.org/10.1111/bj.12784>.
- Guallar, S., and Jovani, R. 2019. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. *Ibis* 162:778–786; <https://doi.org/10.1111/ibi.12798>.
- Guallar, S. X., Rueda-Hernández, R. and Pyle, P. 2021. Evolution of the preformative moult in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138:1–14; <https://doi.org/10.1093/ornithology/ukaa070>.
- Hussell, D. J. T. 1991. Fall migrations of Alder and Willow Flycatchers in southern Ontario. *J. Field Ornithol.* 62:260–270.
- Jenni, L., and Winkler, R. 2020. *Moult and Ageing of European Passerines*, 2nd ed. Helm Bloomsbury, London.
- Kelly, J. F., Johnson, M. J., Langridge, S., and Whitfield, M. 2008. Efficiency of stable isotope ratios in assigning endangered migrants to breeding and wintering sites. *Ecol. Appl.* 18:568–576; <https://doi.org/10.1890/07-0027.1>.
- Loffland, H. L., Schofield, L. N., and Siegel, R. B. 2022. Sierra Nevada Willow Flycatcher decline continues but losses abate at two restored meadows. *W. Birds* 53:52–69; <https://doi.org/10.21199/WB53.1.5>.
- Mahoney, S. M., Reudink, M. W., Pasch, B., and Theimer, T. C. 2020. Song but not plumage varies geographically among Willow Flycatcher *Empidonax traillii* subspecies. *J. Avian Biol.* 2020:e02621; <https://doi.org/10.1111/jav.02621>.
- Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J., and Reudink, M. W. 2020. Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. *Biol. Lett.* 16, 20200155; <http://doi.org/10.1098/rsbl.2020.0155>.
- Paxton, E. H., Sogge, M. K., Koronkiewicz, T. J., McLeod, M. A., and Theimer, T. C. 2010. Geographic variation in the plumage coloration of Willow Flycatchers *Empidonax traillii*. *J. Avian Biol.* 41:128–138; <https://doi.org/10.1111/j.1600-048X.2009.04773.x>.
- Pyle, P. 1997a. *Identification Guide to North American Birds*, part 1. Slate Creek Press, Bolinas, CA.
- Pyle, P. 1997b. Molt limits in North American passerines. *N. Am. Bird Bander* 22:49–90.
- Pyle, P. 1998. Eccentric first-year molts in certain tyrannid flycatchers. *W. Birds* 29:29–35.
- Pyle, P. 2008. *Identification Guide to North American Birds*, part 2. Slate Creek Press, Point Reyes Station, CA.
- Pyle, P. 2013. Molt homologies in ducks and other birds: A response to Hawkins (2011) and further thoughts on molt terminology in ducks. *Waterbirds* 36:75–79; <https://doi.org/10.1675/063.036.0111>.
- Pyle, P. 2022a. Defining molts in migratory birds: A sequence-based approach. *J. Avian Biol.* e02958; <https://doi.org/10.1111/jav.02958>; <https://doi.org/10.1111/jav.02958>.
- Pyle, P. 2022b. Examination of digital images from Macaulay Library to determine avian molt strategies: A case study on molts and plumages in eight species of North American hummingbirds. *Wilson J. Ornithol.* 134:52–65; <https://doi.org/10.1676/21-00012>.
- Pyle, P., Leitner, W. A., Lozano-Angulo, L., Avilez-Teran, F., Swanson, H., Gómez-Limón, E., and Chambers, M. K. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111:583–590; <https://doi.org/10.1525/cond.2009.090085>.
- Pyle, P., Saracco, J. F., and DeSante, D. F. 2018a. Evidence of widespread movements from breeding to molting grounds by North American landbirds. *Auk* 135:506–520; <https://doi.org/10.1642/AUK-17-201.1>.

- Pyle, P., Ayyash, A., and Bartosik, M. B. 2018b. Replacement of primaries during prealternate molts in North American *Larus* gulls. *W. Birds* 49:293–306; <https://doi.org/10.21199/WB49.4.9>.
- Pyle, P., Foster, K. R., Godwin, C. M., Kaschube, D. R., and Saracco, J. F. 2020. Yearling proportion correlates with habitat structure in a boreal forest landbird community. *PeerJ* 8:e8898; <https://doi.org/10.7717/peerj.8898>.
- Pyle, P., Gahbauer, M., Johnson, E. I., Ryder, T. B., and Wolfe, J. D. 2022. Application of a global age-coding system (“WRP”), based on molts and plumages, for use in demographic and other studies of birds. *Ornithology* 139:1–12; <https://doi.org/10.1093/ornithology/ukab063>.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; <https://www.R-project.org/>.
- Rohwer, S., Butler, L. K., and Froehlich, D. R. 2005. Ecology and demography of east–west differences in molt scheduling of neotropical migrant passerines, in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, eds.), pp. 87–105. Johns Hopkins Univ. Press, Baltimore.
- Ruegg, K., Bay, R. A., Anderson, E. C., Saracco, J. F., Harrigan, R. J., Whitfield, M., Paxton, E. H., and Smith, T. B. 2018. Ecological genomics predicts climate vulnerability in an endangered southwestern songbird. *Ecol. Lett.* 21:1085–1096; <https://doi.org/10.1111/ele.12977>.
- Ruegg, K., Anderson, E. C., Somveille, M., Bay, R. A., Whitfield, M., Paxton, E. H., and Smith, T. B. 2021. Linking climate niches across seasons to assess population vulnerability in a migratory bird. *Global Change Biol.* 27:3519–3531; <https://doi.org/10.1111/gcb.15639>.
- Sedgwick, J. A. 2020. Willow Flycatcher (*Empidonax traillii*), version 1.0, in *Birds of the World* (A. F. Poole and F. B. Gill, eds.). Cornell Lab Ornithol., Ithaca, NY; <https://doi.org/10.2173/bow.wilfly.01>.
- Terrill, R. S., Seeholzer, G. F. and Wolfe, J. D. 2020. Evolution of breeding plumages in birds: A multiple-step pathway to seasonal dichromatism in new world warblers (Aves: Parulidae). *Ecol. Evol.* 10:9223–9239; <https://doi.org/10.1002/ece3.6606>.
- United States Fish and Wildlife Service (USFWS). 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. *Federal Register* 60:10694–10715.
- Unitt, P. 1987. *Empidonax traillii extimus*: An endangered subspecies. *W. Birds* 18:137–162.
- Voelker, G., and Rohwer, S. 1998. Contrasts in scheduling of molt and migration in eastern and western warbling-vireos. *Auk* 115:142–155; <https://doi.org/10.2307/4089119>.
- Whitfield, M. J., and Sogge, M. K. 1999. Range-wide impact of Brown-headed Cowbird parasitism on the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). *Studies Avian Biol.* 18:182–190.
- Willoughby, E. J. 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. W. Found. Vert. Zool.* 4:247–286.
- Wolfe, J. D., Ryder, T. B., and Pyle, P. 2010. Using molt cycles to categorize the age of tropical birds: An integrative system. *J. Field Ornithol.* 81:186–194; <https://doi.org/10.1111/j.1557-9263.2010.00276.x>.
- Yuri, T., and Rohwer, S. 1997. Molt and migration in the Northern Rough-winged Swallow. *Auk* 114:249–262; <https://doi.org/10.2307/4089166>.

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