



## Clarification of molt strategies in three Empidonax flycatchers

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Clarification of molt strategies in three *Empidonax* flycatchersBlaine H. Carnes,<sup>1\*</sup> Christine M. Godwin,<sup>2</sup> Kenneth R. Foster,<sup>2</sup> and Peter Pyle<sup>3</sup>

**ABSTRACT**—We studied plumages and molt patterns of Yellow-bellied (*Empidonax flaviventris*), Least (*E. minimus*), and Alder (*E. alnorum*) flycatchers, primarily on the breeding grounds but with additional data from wintering grounds and a migration stopover site, in order to clarify our knowledge of molt strategies in these species. We determined that these 3 species have a similar overall molt strategy: (1) a partial-to-incomplete preformative molt begun on the breeding grounds, suspended over migration, and completed on the wintering grounds; (2) a limited-to-partial first prealternate molt on the wintering grounds that can overlap the final stages of the preformative molt; (3) a complete definitive prebasic molt begun on summer grounds and completed on wintering grounds; and (4) a limited-to-partial definitive prealternate molt that may overlap with the final stages of the prebasic molt. Our study clarifies previous terminologies and allows these molts to be interpreted in an evolutionary framework. We suggest that observed differences in molt extents among species may be linked to differences in wintering latitude and habitat. The broadleaf forest preferred by Yellow-bellied Flycatcher likely retains insect biomass later into the winter season than the scrub habitat preferred by Least Flycatcher, and this may promote more extensive preformative feather replacement in that species. The much more extensive preformative molt of Alder Flycatcher may be due to its wintering farther south, where there is greater annual solar exposure, perhaps resulting in higher rates of feather degradation. Our data also suggest that the extent of prealternate molt in these species may vary with proximate factors on the winter grounds affecting individuals, rather than body condition at the beginning of winter. Received 11 September 2020. Accepted 18 May 2021.

**Key words:** molt strategy, molt suspension, Neotropical migrants, prealternate, preformative.

**Aclaración de estrategias de muda en 3 especies de mosqueros *Empidonax***

**RESUMEN** (Spanish)—Estudiamos el plumaje y los patrones de muda en los mosqueros *Empidonax flaviventris*, *E. minimus* y *E. alnorum*, principalmente en las áreas de reproducción pero con datos adicionales de las áreas de invernada y un sitio de migración, para aclarar nuestro conocimiento de las estrategias de muda en estas especies. Determinamos que estas 3 especies tienen una estrategia de muda general similar: 1) una muda preformativa de parcial a incompleta comenzada en las zonas de reproducción, suspendida durante la migración y completada en las zonas de invernada; 2) una muda prealternativa primera limitada a parcial en las zonas de invernada que puede superponerse a las etapas finales de la muda preformativa; 3) una muda prebásica definitiva completa iniciada en zonas de verano y completada en zonas de invernada; y 4) una muda prealternativa definitiva limitada a parcial que ocasionalmente puede superponerse a las etapas finales de la muda prebásica. Nuestro estudio aclara terminologías anteriores y permite interpretar estas mudas en un marco evolutivo. Sugerimos que las diferencias observadas en la extensión de la muda entre las especies pueden estar relacionadas con diferencias en la latitud y el hábitat de invernada. El bosque de hoja ancha preferido por *E. flaviventris* probablemente retiene la biomasa de insectos más tarde en la temporada de invierno que el hábitat de matorrales preferido por *E. minimus*, y esto puede promover un reemplazo de plumas preformativo más extenso en esa especie. La muda preformativa mucho más extensa de *E. alnorum* puede deberse a su invernada más al sur, donde hay una mayor exposición solar anual, lo que tal vez resulte en tasas más altas de degradación de las plumas. Nuestros datos también sugieren que la extensión de la muda prealternativa en estas especies puede variar con factores próximos en los terrenos invernales que afectan a los individuos, más que la condición corporal al comienzo del invierno.

**Palabras clave:** estrategia de muda, migratorias Neotropicales, prealternativa, preformativa, suspensión de muda.

Molt cycles and their relationship to plumage differences may have an underappreciated role in explaining patterns of avian behavior (Greenberg and Gradwohl 1997), post-breeding ecology (Vitz and Rodewald 2006, Pyle et al. 2020), survivorship (Saracco et al. 2010), and population trends (Albert et al. 2016). Although the study of molt and plumages is relatively advanced in North America (Pyle 1997a, 1997b), the timing and

extent of molts that occur on nonbreeding grounds of Neotropical migrants are not as well known. Several recent studies of common migratory species have revealed more extensive molt than previously known (Pyle and Kayhart 2010, Wolfe and Pyle 2011). In addition, previously unknown molts have been detected and described (Dittmann and Cardiff 2009, Sieburth and Pyle 2018).

In *Empidonax* flycatchers, 9 of 11 North American breeding species molt on the nonbreeding grounds, either at stopover locations in fall migration or on the winter grounds (Pyle 1997a, Pyle et al. 2018). However, our understanding of molts that occur in Central and South America remains very limited (Rueda-Hernández et al. 2018). In Yellow-bellied (*Empidonax flaviventris*)

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and Least (*E. minimus*) flycatchers, molt has been reported to follow the Complex Alternate Strategy (Pyle 1997a, Howell et al. 2003, Howell 2010). Molts in Yellow-bellied Flycatcher have been reported to include a limited preformative molt taking place on the summer grounds, an incomplete and eccentric prealternate molt taking place on the winter grounds, and incomplete definitive prebasic and definitive prealternate molts taking place on the winter grounds (Pyle 1997a, 1997b).

Molts in Least Flycatcher have been reported as including a partial preformative molt occurring on summer grounds, complete prebasic molts that can suspend over migration, and partial-to-incomplete first prealternate molts that occur on the winter grounds. In Alder Flycatcher (*E. alnorum*), by contrast, molts have been reported to take place on the winter grounds and follow the Complex Basic Strategy (Johnson 1963), with incomplete preformative molts in which all feathers but the primary coverts are replaced, and complete definitive prebasic molts. However, the possible occurrence of a prealternate molt in Alder Flycatcher has been suggested (Pyle 1997a). The terminology of these reported molts was based largely on timing and location of molts, which can inhibit an understanding of those that take place on nonbreeding grounds (Jenni and Winkler 2020, Guallar et al. 2021).

In order to clarify the molt patterns and ageing criteria used with these species, we studied Yellow-bellied, Least, and Alder flycatchers on their breeding grounds in northeastern Alberta, Canada. We assessed the number of molted feathers visible in close-up digital images of the body plumage and of the dorsal aspect of wings and tails. This enabled us to make a quantitative assessment of the formative, basic, and alternate feather generations. We also interpret our results using the approach of Humphrey and Parkes (1959) and Howell et al. (2003), by defining molts based on how they evolved from ancestral species of Tyrannidae, allowing these molts to be compared in a much clearer interpretive framework.

## Methods

We collected molt data while conducting banding as part of the Monitoring Avian Productivity and Survivorship (MAPS) program, a cooperative effort among public agencies, private

organizations, and bird banders to provide long-term data on demographic parameters and vital rates for landbird species of North America (Saracco et al. 2008; DeSante et al. 2015, 2019). We collected most of our data in connection with the Boreal MAPS project located in the Oil Sands Region of northeastern Alberta (Foster et al. 2012, 2017; Pyle et al. 2020). Habitats of varying age and complexity across the boreal region comprised our study sites. We collected data from the second week of June through the first week of August. One author (BHC) collected additional data for Least and Yellow-bellied flycatchers while participating in a fall migration banding program in eastern Maryland and a winter banding program in Belize (Central America).

We analyzed feather replacement patterns by age class on birds captured during the Boreal MAPS program from 2011 to 2019. Age determination to hatching year (HY), second year (SY), and after second year (ASY) followed the criteria of Pyle (1997a). Whenever possible, we took photographs of the right wing, tail, and body of captured SY and ASY *Empidonax* flycatchers. We examined these photographs to verify age determinations and to record the extent of inserted preformative and prealternate molts. Our goal was to describe which feathers had been replaced within the remiges, greater coverts, primary coverts, and rectrices during each of these molts. In first-cycle birds (SYs), we categorized replaced feathers as either formative or first alternate based primarily on position and degree of feather wear. Primaries are numbered distally (innermost to outermost), and secondaries are numbered proximally (outermost to innermost), following Pyle (1997a). We assumed that replacement among coverts was distal within each tract, and that the tertials were replaced in sequence s8–s9–s7 (Pyle 1997a, 1997b, 2013). Markedly less worn feathers within a group of formative feathers that are typically replaced first in the molt sequence for that group (e.g., inner greater coverts, s8) were considered to be first alternate and assumed to have also been replaced during the previous preformative molt. We recorded extent of body-feather molt as none (0), trace (1), light (2), medium (3), or heavy (4), according to the MAPS protocol (DeSante et al. 2019). We scored preformative body-feather molt in HYs only for individuals that appeared to have completed their prejuvenile molt.

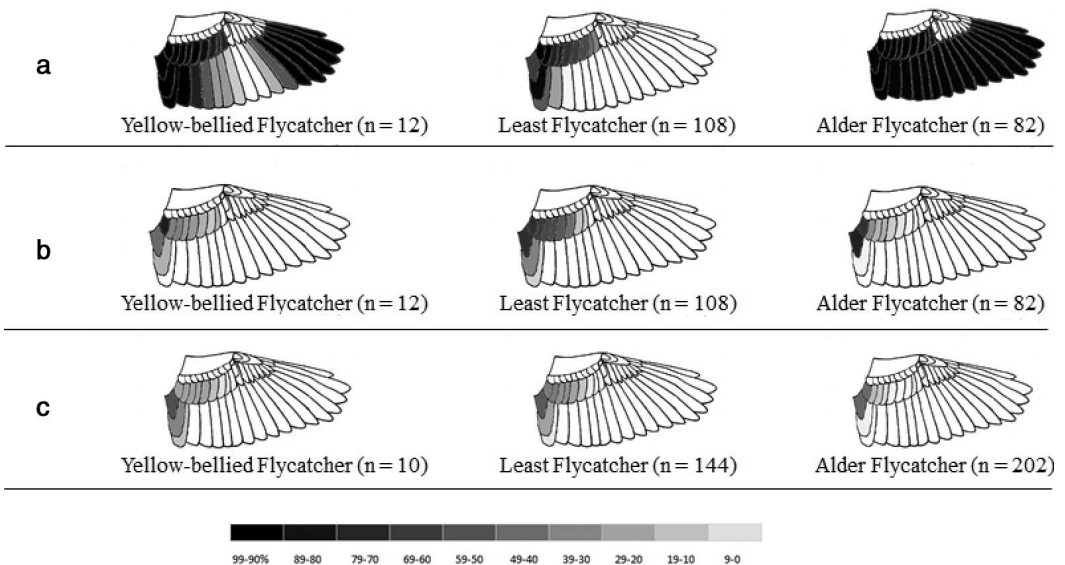
**Table 1.** Mean number of feathers replaced within the remiges and coverts during inserted preformative (PF), first prealternate (PA1), and definitive prealternate (DPA) molts in Yellow-bellied (YBFL), Least (LEFL), and Alder (ALFL) flycatchers captured on the summer grounds in northeastern Alberta, Canada.

Species	Molt	<i>n</i>	Greater coverts	Secondaries	Primaries	Primary coverts	Total
<b>YBFL</b>	PF	12	9.17	6.42	6.83	0	22.42 ± 2.68
	PA1	12	2.58	0.75	0	0	3.33 ± 2.27
	DPA	10	1.90	1.20	0	0	3.10 ± 3.70
<b>LEFL</b>	PF	108	6.91	2.56	0	0	9.47 ± 3.20
	PA1	108	4.03	1.31	0	0	5.33 ± 2.56
	DPA	144	2.14	0.96	0	0	3.10 ± 3.20
<b>ALFL</b>	PF	82	9.83	8.67	9.63	0	28.17 ± 3.53
	PA1	82	1.70	0.50	0	0	2.20 ± 1.67
	DPA	202	1.10	0.57	0	0	1.67 ± 1.88

We analyzed the extent of preformative, first prealternate, and definitive prealternate molts using generalized linear models implemented through the open source program R (R Core Team 2020). Each model contained species and sex as fixed effects. Feather count data were modeled as a Poisson distribution. In addition, a Spearman rank correlation analysis was conducted on the preformative and first prealternate molts of SY birds of each species to determine if the extent of the 2 molts were similar. A significance level of  $P \leq 0.05$  was used for all statistical tests.

## Results

The extents for inserted molts in our 3 study species are summarized in Table 1 and Figures 1 and 2. The 3 species differed significantly from one another in extent of the preformative molt (Tables 1–2, Fig. 1a, 2a–d): Least Flycatcher replaced no primaries but up to 5 inner secondaries, Yellow-bellied Flycatcher replaced up to 7 outer primaries and all secondaries in an eccentric pattern, and most Alder Flycatchers (96.3%) replaced all remiges and all rectrices (Table 1). However, 3 Alder Flycatchers (3.7%) underwent



**Figure 1.** Frequency of replacement in the greater coverts and remiges in the preformative (a), first prealternate (b), and definitive prealternate (c) molts of Yellow-bellied, Least, and Alder flycatchers. Gray scales represent observed replacement frequencies (note lesser and median coverts not scored).



**Figure 2.** Examples of molts in Yellow-bellied, Least, and Alder flycatchers. (a) Extent of preformative molt in Yellow-bellied Flycatcher on 13 December, after resuming molt on the winter grounds. Formative feathers include lesser, median, and greater coverts, and secondary 8. (b) Eccentric preformative molt overlapping with the first prealternate molt in Yellow-bellied Flycatcher on 31 March on the winter grounds. Primaries 4–8 (but not corresponding primary coverts) are in active preformative molt and inner greater coverts are in active prealternate molt. (c) First prealternate and preformative molt extents in Least Flycatcher on 11 June on the summer grounds. First alternate feathers include secondary 9, inner greater coverts, and inner median coverts; formative feathers include secondaries 6–8 and middle greater covert; juvenile feathers include outer greater coverts, primary coverts, and remainder of remiges. (d) First prealternate and preformative molt extents in Alder Flycatcher on 11 July on the summer grounds. Secondary 9 is alternate; lesser, median, and greater coverts, and all remaining remiges, are formative; primary coverts are juvenile. (e) Definitive prealternate molt extent in Alder Flycatcher on 21 June on the summer grounds. Definitive alternate feathers include the innermost greater covert and secondaries 8–9. (f) Partial preformative molt extent shown by Alder Flycatcher on 23 June on the breeding grounds. Secondaries 8–9 and greater covert 7 are alternate; the outer 2 greater coverts, primary coverts, and remaining remiges are juvenile; all other feathers are formative.

only a partial preformative molt including 8–10 greater coverts and s8–9, but no other remiges or rectrices (Fig. 2f). No birds were observed to replace any primary coverts during the preformative molt.

All 3 species appeared to suspend the preformative molt over fall migration. Our data on HYS

of these species indicate that 90% of 10 Yellow-bellied, 88% of 169 Least, and 55% of 125 Alder flycatchers began replacement of juvenile body feathers prior to completion of the MAPS season on 8 August. Additional preformative molt replacement of body feathers and wing coverts might be possible in mid-August through early

**Table 2.** Estimated coefficients for the Poisson regression of the total number of feathers replaced in the preformative, first prealternate, and definitive prealternate molts of Yellow-bellied (YBFL), Least (LEFL), and Alder (ALFL) flycatchers.

Variable	Estimate	SE	Z	P
<b>Preformative</b>				
Intercept (ALFL)	3.3560	0.0321	104.599	<0.001
LEFL	-1.0877	0.0381	-28.528	<0.001
YBFL	-0.2289	0.0646	-3.542	<0.001
<b>First prealternate</b>				
Intercept (ALFL)	0.6171	0.0939	6.569	<0.001
LEFL	0.9372	0.0869	10.790	<0.001
YBFL	0.4373	0.1756	2.491	0.013
<b>Definitive prealternate</b>				
Intercept (ALFL)	0.26561	0.0874	3.039	0.002
LEFL	0.68447	0.0768	8.913	<0.001
YBFL	0.58947	0.1878	3.139	0.002

September, after completion of MAPS data collection but before southbound migration. Based on captures during fall migration and early winter, prior to suspending molt for migration, the preformative molts of Yellow-bellied and Least flycatchers can include a variable number of inner greater coverts and 0–3 tertials, but no other remiges (Fig. 1a). These species then resume the preformative molt on the winter grounds, replacing additional greater coverts as well as tertials and some inner secondaries in Least Flycatcher, and inner secondaries and outer primaries in Yellow-bellied Flycatcher (Fig. 1b). Individuals of all 3 species can also suspend the prebasic molt of body feathers over fall migration; our data indicate that 50% of Yellow-bellied and Least flycatchers, and 52% of Alder Flycatchers, had begun body feather molt prior to the end of the MAPS season.

The first and definitive prealternate molts are partial in all 3 species (Tables 1–3, Fig. 1b–c, 2b–e). The number of feathers replaced in the first and definitive prealternate molts was significantly different in Alder and Least flycatchers (Table 3), with more feathers replaced during the first prealternate molt than in subsequent definitive prealternate molts (Table 1); this difference was largest for Least Flycatcher. Yellow-bellied Flycatcher did not show differences in extent between these 2 molts.

We found no correlation between the extent of the preformative and first prealternate molts of wing coverts or tertials for Least Flycatcher ( $r_{s(n=105)} =$

**Table 3.** Estimated coefficients for the Poisson regression of the total number of feathers replaced in the first prealternate and definitive prealternate molts by age in Yellow-bellied (YBFL), Least (LEFL), and Alder (ALFL) flycatchers.

Variable	Estimate	SE	z	P
ALFL Intercept (ASY)	0.5259	0.0546	9.625	< 0.001
SY	0.2445	0.0933	2.621	0.009
LEFL Intercept (ASY)	1.1082	0.0487	22.738	< 0.001
SY	0.5765	0.0644	8.957	< 0.001
YBFL Intercept (ASY)	1.1314	0.1796	6.300	< 0.001
SY	0.0726	0.2393	0.303	0.76

$-0.0542$ ,  $P = 0.58$ ) or Alder Flycatcher ( $r_{s(n=81)} = -0.1617$ ,  $P = 0.14$ ). In Yellow-bellied Flycatcher, however, the preformative and first prealternate molts were negatively correlated ( $r_{s(n=12)} = -0.6541$ ,  $P = 0.021$ ), meaning birds with a more extensive preformative molt had a less extensive prealternate molt and vice versa. We found no differences in molt extent by sex in any of the 3 species.

## Discussion

Our study shows that Yellow-bellied, Least, and Alder flycatchers have broadly similar molt strategies that include (1) a partial-to-incomplete preformative molt begun on the breeding grounds, suspended over migration, and completed on the wintering grounds; (2) a limited-to-partial first prealternate molt on the wintering grounds that can overlap the final stages of the preformative molt; (3) a complete definitive prebasic molt begun on summer grounds and completed on wintering grounds; and (4) a limited-to-partial definitive prealternate molt that may occasionally overlap the final stages of the prebasic molt. Our data, together with studies of molt extents in migratory stopover locations (Colorado 2010), indicate that in all 3 species preformative and prebasic molts typically suspend for southbound migration, and that their prealternate molts occur on the wintering grounds.

Pyle (1997a, 1997b) interpreted the molt strategy of Yellow-bellied Flycatcher as consisting of a limited preformative molt on the breeding grounds; an incomplete, eccentric first prealternate; and incomplete definitive prebasic and prealternate molts, all taking place on the wintering grounds. This interpretation followed that of

other authors using older European-based terminology defining molts relative to timing of breeding (e.g., Dwight 1900, Dickey and van Rossem 1938, Mengel 1952, Johnson 1963, Oberholser 1974, Hussell 1982). By comparing these molts with other tyrannid species such as the more basal genera *Myiarchus* and *Tyrannus* (Rheindt et al. 2008) in an evolutionary sense, however, we propose that best application of molt terminology according to the Humphrey and Parkes (1959) system would consider the preformative molt to be suspended over fall migration and protracted through spring to include primaries and secondaries and the definitive prebasic molt to be complete, with some individuals suspending body molt over migration and not completing flight-feather molt until spring. In both cases, final growth of formative and basic remiges can overlap the partial prealternate molt. For example, prealternate body and wing-covert replacement can commence or occur while outer primaries are still growing during the eccentric preformative molt in Yellow-bellied Flycatcher (Fig. 2b).

Similarly, the preformative molt in Least Flycatcher appears to be more extensive than previously thought, with regular replacement of wing coverts, tertials, and occasionally inner secondaries. Again, lack of consideration of preformative molt suspension by previous authors may explain former descriptions of the preformative molt in Least Flycatcher as including only a few wing coverts (Johnson 1963). Recognizing that the molt is suspended, it becomes more evident that Least and Yellow-bellied flycatchers share several similarities in pattern and timing of the preformative molt with each other and with many other migratory North American flycatchers and passerines (Pyle 1997a, 1998).

Aside from Foster (2007) and Areta et al. (2016), which give cursory attention to molt, there is essentially no published information on timing and duration of molts on the winter grounds in Alder Flycatcher, as much of their wintering range in the western Amazon basin is subject to heavy rains from November to May (Lowther 1999, Areta et al. 2016). Our results for this species indicate that preformative and definitive prebasic molts are suspended prior to fall migration in similar fashion to Yellow-bellied and Least flycatchers (Hussell 1991). Our analysis of feather wear among greater coverts and remiges suggests

that preformative and definitive prebasic molts in Alder Flycatcher resume soon after arrival on the winter grounds (Foster 2007) but take place mainly between January and March (Pyle 1997a, Areta et al. 2016), as documented in the closely related Willow Flycatcher (*E. traillii*) by Dickey and van Rossem (1938). Our results also confirm the speculation of Pyle (1997a) that partial prealternate molts occur. We predict that these molts primarily take place in March–April and may overlap the conclusion of the preformative and definitive prebasic molts, as we suggest for first-year Yellow-bellied Flycatcher. We propose that the rare Alder Flycatcher individuals that retain remiges in the preformative molt are from late broods and/or are in poor body condition upon arrival on the winter grounds. The fact that no eccentric molts were observed suggests either (1) that there may be a fixed mechanism that triggers the remigial molt to be either partial or near-complete, or (2) that there may be a facultative mechanism for suspending the molt prior to completion.

Despite these species' similarities in overall molt strategy, we observed differences among them in molt extent. Compared to Least Flycatcher, Alder Flycatcher exhibits more extensive preformative and less extensive prealternate molts, while molt extents in Yellow-bellied Flycatcher fall between the other 2 species. These differences may be linked to differences in wintering latitude and habitat. Both Yellow-bellied and Least flycatchers winter primarily in Mexico and Central America, but their habitat preferences differ, with Yellow-bellied Flycatcher mainly found in tall broadleaf forests (Dickey and van Rossem 1938, Gross and Lowther 2011) and Least Flycatcher more often inhabiting open scrub habitats (Tarof and Briskie 2008). The more-extensive preformative molt in Yellow-bellied Flycatcher is at odds with predictions that humid forest-dwelling species should have less-extensive molts than those of open scrub habitats, if harsher vegetation and increased solar radiation causes increased wear in feathers, requiring them to be replaced more often for functional purposes (Willoughby 1991; Pyle 1998, 2008; Guallar et al. 2021). However, across much of the wintering grounds of Yellow-bellied and Least flycatchers, there is a pronounced dry season that begins partway through the northern winter and intensifies until spring migration (Tarof

and Briskie 2008, Gross and Lowther 2011). The moister forests preferred by Yellow-bellied Flycatcher likely retain moisture and insect biomass further into the winter than the scrub habitats preferred by Least Flycatcher, as shown by other dry forest/scrub habitats in the northern Neotropics (Marra and Holmes 2001), and this may promote more extensive preformative feather replacement in Yellow-bellied Flycatcher.

Alder Flycatcher, which winters in South America, prefers exposed shrubby habitats like Least Flycatcher (Lowther 1999, Tarof and Briskie 2008), implying that their molts should be similar in extent, but we suggest that both the later timing of the preformative and prebasic molts and the greater extent of the preformative molt in Alder Flycatcher may result from a more-southerly wintering latitude (Pyle 1998, Guallar et al. 2021). This latitude effect relates to increased annual solar radiation for birds that winter at tropical and southern temperate latitudes during the boreal winter (Rohwer et al. 2005), as has been proposed for shorebirds wintering at different latitudes (Pyle 2008: p. 500–505), even within species (Serra 2001), as well as for migratory New World warblers (Terrill et al. 2020). Additionally, in contrast to the dry season that occurs on the winter grounds of Yellow-bellied and Least flycatchers, the northern winter is the wettest portion of the year on much of the Alder Flycatcher wintering grounds (Lowther 1999). A precipitation-induced flush of insect biomass may support a more extensive preformative molt in Alder Flycatcher, while preformative molts in Yellow-bellied and Least flycatchers may be constrained by comparatively limited resources.

Yellow-bellied Flycatcher showed a negative correlation between the extent of the preformative and first prealternate molts, as would be expected if feather wear and energetic constraints drive molt patterns. Individuals that undergo a more extensive preformative molt likely have less need to replace feathers in the prealternate molt, especially as the timing of eccentric preformative remex replacement can overlap with the prealternate molt in this species. Contrastingly, first-cycle individuals in Least and Alder flycatchers did not show correlations between extents of their preformative and first prealternate molts. This suggests that individual variation in extent of the prealternate molt in these 2 species can stem from variation in

proximal factors on the winter grounds (e.g., weather events or food resources), rather than early-winter condition of individuals, as in other migratory passerines that can show variation in timing of the prealternate molt (Danner et al. 2015). Additionally, in Least and Alder flycatchers, the first prealternate molt is more extensive than subsequent prealternate molts, which may result from a need to replace a higher percentage of lower-quality juvenile feathers than higher-quality basic feathers during inserted molts (Greenwood et al. 1983, Pyle 1997a, Kiat and Izhaki 2016). The absence of a similar difference in Yellow-bellied Flycatcher may reflect a different molt strategy or may be the effect of the small sample size for this species.

The protracted molts following suspension in these 3 *Empidonax* species bear resemblance to molt strategies found in many Neotropical species (Pyle 1997a, Johnson and Wolfe 2017). The lack of oncoming winter conditions reduces temporal constraints on molt in tropical species, resulting in slower feather growth rates than what is found in temperate species of similar size (Pyle 2008, Johnson et al. 2012). With a few exceptions, many of the taxa closest to *Empidonax* in the Tyrannidae (e.g., some *Contopus*, *Mitrephanes*) are tropical and nonmigratory (Cicero and Johnson 2002, Ohlson et al. 2008, Rheindt et al. 2008), and the 3 *Empidonax* discussed here, as they evolved a migratory strategy, may have also evolved suspended molts across migration as a way to reduce energetic demands.

An examination of molts in tropical species of *Empidonax* flycatchers could further help determine the relationship between molt extent, habitat, and latitude. Initial work by Johnson (1974) comparing molts of Pacific-slope (*E. difficilis*), Cordilleran (*E. occidentalis*), and Yellowish (*E. flavescens*) flycatchers indicated that the preformative molt of Yellowish Flycatcher includes minimal replacement of wing coverts and secondaries, but regular replacement of rectrices, and no obvious prealternate molts. However, Johnson (1974) concluded the prealternate molts of Pacific-slope Flycatcher are confined to a few body feathers, contrary to recent photographic evidence from MAPS banding stations (BHC, 2015, unpubl. data). Like other early evaluations of molt in *Empidonax* using seasonally based molt terminol-



ogies, we believe that reevaluation in an evolutionary context is needed.

We encourage ornithologists working in tropical regions to collect molt-related data and, whenever possible, for banding programs to collect standardized wing and tail photos and contribute them to online resources such as Environment and Climate Change Canada's Piranga catalogue. This enables detailed molt data to be collated at a later time, and, in turn, might yield new insights into molt patterns and timing even in well-studied species (Carnes 2017, Carnes and Ash 2019). In addition, photographs could serve as vouchers for published molt data, with later review allowing for verification of age, sex, and even species identification.

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#### Literature cited

- Albert SK, DeSante DF, Kaschube DR, Saracco JF. 2016. MAPS (Monitoring Avian Productivity and Survivorship) data provide inferences on demographic drivers of population trends for 158 species of North American landbirds. *North American Bird Bander*. 41:133–140.
- Areta JI, Mangini GG, Gandoy FA, Gorleri F, Gomez D, et al. 2016. Ecology and behavior of Alder Flycatchers (*Empidonax alnorum*) on their wintering grounds in Argentina. *Wilson Journal of Ornithology*. 128:830–845.
- Carnes BH. 2017. Age determination of Swainson's Thrush using the distal marginal coverts. *North American Bird Bander*. 42:104–107.
- Carnes BH, Ash A. 2019. First evidence for suspension of prebasic molt in a White-eyed Vireo. *Western Birds*. 50:52–54.
- Cicero C, Johnson NK. 2002. Phylogeny and character evolution in the *Empidonax* group of Tyrant Flycatchers (Aves: Tyrannidae): A test of W. E. Lanyon's hypothesis using mtDNA sequences. *Molecular Phylogenetics and Evolution*. 22:289–302.
- Colorado GJ. 2010. Fall migration of *Empidonax* flycatchers in northwestern Colombia. *Journal of Field Ornithology*. 81:259–266.
- Danner RM, Greenberg RS, Danner JE, Walters JR. 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. *Functional Ecology*. 29:259–267.
- DeSante DF, Burton KM, Velez P, Froehlich D. 2019. MAPS manual. Point Reyes Station (CA): The Institute for Bird Populations. [http://www.birdpop.org/docs/pubs/DeSante\\_et\\_al\\_MAPS\\_Manual\\_2015.pdf](http://www.birdpop.org/docs/pubs/DeSante_et_al_MAPS_Manual_2015.pdf)
- DeSante DF, Kaschube DR, Saracco JF. 2015. Vital rates of North American landbirds. Point Reyes Station (CA): The Institute for Bird Populations. [www.VitalRatesOfNorthAmericanLandbirds.org](http://www.VitalRatesOfNorthAmericanLandbirds.org)
- Dickey DR, van Rossem AJ. 1938. The birds of El Salvador. Chicago (IL): Field Museum of Natural History, Zoological Series.
- Dittmann DL, Cardiff SW. 2009. The alternate plumage of the Ruby-throated Hummingbird. *Birding*. 41:32–35.
- Dwight J Jr. 1900. The sequences of plumages and moults of the passerine birds of New York. *Annals of the New York Academy of Science*. 13:73–360.
- Foster KR, Godwin CM, Pyle P. 2012. Monitoring avian productivity and survivorship in the oil sands region of northeastern Alberta. In: Fourie AB, Tibbett M, editors. Mine closure 2012. Perth (Australia): Australian Centre for Geomechanics; p. 563–571.
- Foster KR, Godwin CM, Pyle P, Saracco JF. 2017. Reclamation and habitat-disturbance effects on land-bird abundance and productivity indices in the oil sands region of northeastern Alberta, Canada. *Restoration Ecology*. 25:532–538.
- Foster MS. 2007. Winter behavior and ecology of the Alder Flycatcher (*Empidonax alnorum*) in Peru. *Omitologia Neotropical*. 18:171–186.
- Greenberg R, Gradwohl J. 1997. Territoriality, adult survival, and dispersal in the Checker-throated Antwren in Panama. *Journal of Avian Biology*. 28:103–110.
- Greenwood H, Weatherhead PJ, Titman RD. 1983. A new age- and sex-specific molt scheme for the Red-winged Blackbird. *Condor*. 85:104–105.
- Gross DA, Lowther PE. 2011. Yellow-bellied Flycatcher (*Empidonax flaviventris*), version 2.0. In: Poole AF, editor. *Birds of North America*. Ithaca (NY): Cornell Lab of Ornithology. <https://doi.org/10.2173/bna.566>
- Guallar S, Rueda-Hernández R, Pyle P. 2021. Evolution of the preformative molt in Cardinalidae correlates with

- transitions from forest to open habitats. *Ornithology*. 138:1–14.
- Howell SNG. 2010. *Molt in North American birds*. Boston (MA): Houghton Mifflin Harcourt.
- Howell SNG, Corben C, Pyle P, Rogers DI. 2003. The first basic problem: A review of molt and plumage homologies. *Condor*. 105:635–653.
- Humphrey PS, Parkes KC. 1959. An approach to the study of molts and plumages. *Auk*. 76:1–31.
- Hussell DJT. 1982. Migration of the Yellow-bellied Flycatcher in southern Ontario. *Journal of Field Ornithology*. 53:223–224.
- Hussell DJT. 1991. Fall migrations of Alder and Willow flycatchers in southern Ontario. *Journal of Field Ornithology*. 62:260–270.
- Jenni L, Winkler R. 2020. *Moult and ageing of European passerines*. London (UK): Bloomsbury Publishing.
- Johnson EI, Stouffer PC, Bierregard RO Jr. 2012. The phenology of molting, breeding, and their overlap in central Amazonian birds. *Journal of Avian Biology*. 43:141–154.
- Johnson EI, Wolfe JD. 2017. *Molt in Neotropical birds: Life history and aging criteria*. Boca Raton (FL): CRC Press.
- Johnson NK. 1963. Comparative molt cycles in the Tyrannid genus *Empidonax*. *Proceedings of the International Ornithological Conference*. 13:870–883.
- Johnson NK. 1974. Molt and age determination in Western and Yellowish flycatchers. *Auk*. 91:111–131.
- Kiat Y, Izhaki I. 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology*. 47:47–56.
- Lowther PE. 1999. Alder Flycatcher (*Empidonax alnorum*), version 2.0. In: Poole AF, Gill FB, editors. *Birds of North America*. Ithaca (NY): Cornell Lab of Ornithology. <https://doi.org/10.2173/bna.446>
- Marra PP, Holmes RT. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk*. 118:92–104.
- Mengel RM. 1952. Certain molts and plumages of Acadian and Yellow-bellied flycatchers. *Auk*. 69:273–283.
- Oberholser HC. 1974. *The bird life of Texas*. Austin (TX): University of Texas Press.
- Ohlson J, Fjeldså J, Ericson PGP. 2008. Tyrant flycatchers coming out in the open: Phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). *Zoological Scripta*. 37:315–335.
- Pyle P. 1997a. Identification guide to North American birds. Part I. Bolinas (CA): Slate Creek Press.
- Pyle P. 1997b. Molt limits in North American passerines. *North American Bird Bander*. 22:49–90.
- Pyle P. 1998. Eccentric first year molt patterns in certain tyrannid flycatchers. *Western Birds*. 29:29–35.
- Pyle P. 2008. Identification guide to North American birds: Part II. Bolinas (CA): Slate Creek Press.
- Pyle P. 2013. Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconiformes) and parrots (Psittaciformes). *Condor*. 115:593–602.
- Pyle P, Foster KR, Godwin CM, Kaschube DR, Saracco JF. 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, Kayhart R. 2010. Replacement of primaries during the prealternate molt of a Yellow Warbler. *North American Bird Bander*. 35:178–181.
- Pyle P, Saracco JF, DeSante DF. 2018. Evidence of widespread movements from breeding to molting grounds in North American landbirds. *Auk: Ornithological Advances*. 135:506–520.
- R Core Team. 2020. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rheindt FE, Norman JA, Christidis L. 2008. Phylogenetic relationships of tyrant-flycatchers (Aves: Tyrannidae), with an emphasis on the elaeniine assemblage. *Molecular Phylogenetics and Evolution*. 46:88–101.
- Rohwer S, Butler LK, Froelich DR. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In: Greenberg R, Marra PP, editors. *Birds of two worlds: The ecology and evolution of migration*. Baltimore (MD): Johns Hopkins University Press; p. 87–105.
- Rueda-Hernández R, Guallar S, Ruiz-Sánchez A, Pyle P. 2018. The molt issue: Where do we go from now? *Ornitología Neotropical*. 29:S1–S2.
- Saracco JF, DeSante DF, Kaschube DR. 2008. Assessing landbird monitoring programs and demographic causes of population trends. *Journal of Wildlife Management*. 72:1665–1673.
- Saracco JF, Royle JA, DeSante DF, Gardner B. 2010. Modeling spatial variation in avian survival and residency probabilities. *Ecology*. 91:1885–1891.
- Serra L. 2001. Duration of primary molt affects primary quality in Grey Plovers *Pluvialis squatarola*. *Journal of Avian Biology*. 32:377–380.
- Sieburth D, Pyle P. 2018. Evidence for a prealternate molt-migration in the Rufous Hummingbird and its implications for the evolution of molts in Apodiformes. *Auk: Ornithological Advances*. 135:495–505.
- Tarof S, Briskie JV. 2008. Least Flycatcher (*Empidonax minimus*), version 2.0. In: Poole AF, editor. *Birds of North America*. Ithaca (NY): Cornell Lab of Ornithology. <https://doi.org/10.2173/bna.99>
- Terrill RS, Seeholzer GF, Wolfe JD. 2020. Evolution of breeding plumages in birds: A multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). *Ecology and Evolution*. 10:9223–9239.
- Vitz AC, Rodewald AD. 2006. Can regenerating clear cuts benefit mature-forest songbirds? An examination of postbreeding ecology. *Biological Conservation*. 127:477–486.
- Willoughby EJ. 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proceedings of the Western Foundation of Vertebrate Zoology*. 4:247–286.
- Wolfe JD, Pyle P. 2011. First evidence for eccentric prealternate molt in the Indigo Bunting (*Passerina cyanea*): Possible implications for adaptive molt strategies. *Western Birds*. 42:257–262.