

1 **Defining Moults in Migratory Birds: A Sequence-based Approach**

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7 **Abstract:** Two broad nomenclatures have emerged to describe moult strategies in birds,
8 the "life-cycle" system which describes moults relative to present-day breeding and other
9 life-history events and the Humphrey-Parkes (H-P) system which reflects the evolution of
10 moults along ancestral lineages. Using either system, challenges have arisen defining
11 strategies in migratory species with more than one moult per year. When all or part of
12 two moults occur in non-breeding areas they may fail to be recognized as two moults or
13 have been discriminated temporally, whether feathers are replaced in fall, winter, or
14 spring. But in some cases feather replacement can span the non-breeding period, and this
15 has resulted in an inability to identify inserted moults and to compare moult strategies
16 between species. Furthermore, recent analyses on factors influencing the extent of the
17 postjuvenile or preformative moults have either confined this moult to the summer
18 grounds or presumed that it can be suspended and resumed on winter grounds, which has
19 lead to quite divergent results. Evolutionarily, the timing, extent, and location of moults
20 are very plastic whereas the sequence in which feathers are replaced is comparatively
21 fixed. As, such, I propose taking an evolutionary approach to define moults on the basis
22 of feather-replacement sequences as opposed to timing or location of replacement,
23 including strategies in which moults can overlap temporally. I provide examples

24 illustrating the functionality of a sequence-based definition in three migratory North
25 American passerines that can undergo feather replacement twice in non breeding areas,
26 and I demonstrate how this system can effectively apply to moults in many other
27 passerine and non-passerine species. I recommend that authors studying the evolutionary
28 drivers of moult strategies in migratory birds adopt a sequence-based approach or
29 carefully consider replacement strategies both prior to and following autumn migration.

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31 **Key words:** evolution, migration, moult extent, moult terminology, suspended moult

32

33 Avian moult strategies are complex, as have been terminologies used by ornithologists to
34 describe them. Two broad nomenclatures have emerged to describe bird moults
35 (summarized by Jenni and Winkler 2020:11-14), the "life-cycle" system (Dwight 1900),
36 currently employed by most authors in the Old World, and the Humphrey-Parkes or "H-
37 P" system (Humphrey and Parkes 1959 as modified by Howell et al. 2003), currently
38 employed by most authors in the New World. These two nomenclatures have different
39 bases of definition, the first describing moults relative to present-day breeding and other
40 life-history events and the second defining moults based on how they evolved along
41 ancestral lineages. Among resident and many migratory bird species, especially those that
42 breed in boreal and north-temperate regions, moults are relatively discrete and easy to
43 define based on these terminologies. However, challenges occur defining moults in
44 migratory species, especially those with more than one moult per year, each of which can
45 occur partially or entirely in non-breeding areas.

46

47 Among those using the life-cycle terminology, differences of opinion exist about whether
48 the postjuvenile and/or postbreeding moults can begin on summer grounds and resume on
49 winter grounds (e.g., Cramp 1988, for the most part) or are restricted to summering
50 grounds, with feather replacement on wintering grounds being assigned to prebreeding
51 moults (e.g., Jenni and Winkler 2020, for some but not all species). These differences
52 have resulted in confusion in describing life-cycle moults in such species as Barred
53 Warbler *Curruca nisoria* or those of the Red-backed Shrike *Lanius collurio* complex
54 including Isabelline *L. isabellinus* and Brown *L. cristatus* shrikes, species which show
55 evidence of moulting feathers twice on wintering grounds (Stresemann and Stresemann
56 1971, Cramp 1988, Hall and Tullberg 2004, Kiat and Perlman 2016, Jenni and Winkler
57 2020, Kiat and Izhaki 2020). Considering such moults on winter grounds as a single
58 prebreeding moult compromises our ability to identify inserted moults and to
59 discriminate and understand moulting strategies. Furthermore, recent analyses on factors
60 influencing the extent of the postjuvenile and preternate moults in passerines have either
61 confined this moult to the summer grounds (Guallar and Figuerola 2016, Delhey et al.
62 2020, Pérez-Granados et al. 2020, Kiat et al. 2021) or presumed that it can resume on
63 winter grounds (Guallar et al. 2021), which has led to quite divergent interpretations of
64 results.

65

66 The H-P system is often portrayed as attempting to define evolutionary homologies (e.g.,
67 Jenni and Winkler 2020) whereas it is better considered as reflecting the end product of
68 moult evolution itself. Although these two characterizations may appear to differ only
69 subtly, the former interpretation would presume guesswork whereas the latter solidifies

70 the definition of moults, despite the fact that their evolutionary histories are only starting
71 to be elucidated with phylogenetic analyses (e.g., Kiat et al. 2019, Terrill et al. 2020,
72 Guallar et al. 2021). The definitive prebasic moult is best regarded as having evolved
73 from ecdysis during an annual (or cyclic) restorative process in reptiles (Howell and Pyle
74 2015, Kiat et al. 2020), and it may be possible that the preformative moult has also
75 evolved from an extra inserted ecdysis event in younger reptiles as their body size grows.
76 These moults are present in the great majority of birds and can be considered ancestral
77 under H-P nomenclature. Within this framework, additional prealternate moults and
78 occasionally third presupplemental moults have evolved and become inserted within the
79 basic cycle (Humphrey and Parkes 1959). Importantly, prealternate and presupplemental
80 moults have emerged at different times along ancestral bird lineages, and are thus not
81 considered homologous throughout all birds (Howell et al. 2003), just within each lineage
82 from the time the moult first evolved. Such an evolutionary approach can be applied to
83 birds globally rather than favouring boreal-breeding species that form the basis of other
84 terminologies.

85

86 Using this approach, moults that commence on or near breeding grounds and complete at
87 stopover moulting grounds (cf. Pyle et al. 2009, 2018a) or on winter grounds are
88 recognized evolutionarily as single moults. Substantial variation in moult timing,
89 location, and extents of moults before and after suspension can occur among closely
90 related species, within species such as Brown Shrike (Cramp 1988), Common
91 Whitethroat *Curruca communis* (Jenni and Winkler 2020), and Warbling Vireo *Vireo*
92 *gilvus* (Voelker and Rohwer 1998), and even within the same individual interannually

93 (Pyle et al. 2009). It is thus clear from an evolutionary perspective that the timing and
94 locations of moults relative to migration are relatively recent adaptive responses to life-
95 history traits and environmental factors (Pyle et al. 2018a, Kiat et al. 2019, Delhey et al.
96 2020, Terrill et al. 2020, Guallar et al. 2021), rather than their being separate moults that
97 have evolved independently at different locations. It follows that the various
98 terminologies used to describe minor or perceived differences in spatial and temporal
99 replacement patterns in some (but not necessarily all) individuals of a species, including
100 "split moults," "interrupted moults," "seasonally divided moults," "interlaced moults,"
101 and in some cases "arrested moults," may represent variations upon a single
102 evolutionarily derived strategy, broadly termed "suspended moults" by Jenni and Winkler
103 (2020) and those now using H-P nomenclature (e.g., Pyle 2008, Tonra and Reudink
104 2018).

105

106 **IDENTIFYING AND INTERPRETING MOULTS**

107 Under either terminology there remains uncertainty in discriminating
108 preformative/postjuvenile or prebasic/postbreeding moults from prealternate/prebreeding
109 moults when feathers are replaced more than once away from breeding grounds. For
110 example, Pyle (1997) considered protracted overwinter flight-feather replacement in both
111 first-year and adult Yellow-bellied Flycatcher *Empidonax flaviventris* and several other
112 species to include prealternate moults whereas a similar replacement strategy in Red-eyed
113 Vireo *Vireo olivaceus* and many waterbirds (Pyle 2008) was considered only to include
114 the prebasic moult. Similarly, Jenni and Winkler (2020) consider moults of some adult
115 swallows, pipits and some populations of Common Whitethroats to be a single suspended

116 postbreeding moult whereas similar moults in, for example, Barred Warbler, other
117 populations of Common Whitethroats, and European Pied Flycatcher *Ficedula hypoleuca*
118 were considered separate postbreeding and prebreeding moults. In some cases, partial
119 post breeding moults on summer grounds followed by complete prebreeding moults on
120 winter grounds have been reported (e.g., for *Acrocephalus* and *Phylloscopus* warblers,
121 Garden Warbler *Sylvia borin*, and Spotted Flycatcher *Muscicapa striata*), but
122 documentation of moults on winter grounds is widely considered sparse, and evidence
123 that these species are replacing feathers twice rather than suspending moults (in some but
124 not all individuals) is thus far inconclusive (Jenni and Winkler 2020). Indeed, further
125 consideration of wear patterns in the feathers of Arctic Warbler *Phylloscopus borealis*
126 suggested the possibility that only one complete and suspended moult occurs per year
127 (Snyder 2008), rather than a partial moult followed by a complete moult as previously
128 reported (Cramp 1992).

129

130 **A SEQUENCE-BASED APPROACH**

131 Evolutionarily, the timing, extent, and location of moults are very plastic whereas the
132 sequence in which feathers are replaced is comparatively fixed (Pyle 2013). During
133 prebasic moults of remiges, the majority of birds follow the "basic sequence" (Ginn and
134 Melville 1983), replacing primaries distally from a node at the innermost primary (P1;
135 see Table 1 for feather numbering) and secondaries bilaterally from a node at the second
136 tertial (T2 in non-passerines or S8 in passerines), proximally from the outermost feather
137 (S1), and in larger diastataxic species, proximally as well from S5 (Pyle 1997, 2005,
138 2008, 2013; Rohwer 2008; Jenni and Winkler 2020). These sequences are well

139 documented in resident bird species and are maintained in those migratory species in
140 which sequence has been studied. When exceptions to these sequences occur, they are
141 usually found among all individuals and species throughout a lineage once evolved (Pyle
142 2013), for example among avian orders Gruiformes, Falconiformes, and Psittiformes,
143 families such as Diomedidae, and passerine species such as Spotted Flycatcher (Pyle
144 2008, 2013; Rohwer and Rohwer 2018; Jenni and Winkler 2020). Rare exceptions to
145 fixed remigial sequences among passerine genera such as *Lanius*, *Locustella*, *Rhipudura*,
146 and *Muscicapa* (Cramp 1988, Junda et al. 2012, Kiat 2017, Jenni and Winkler 2020) are
147 perhaps best considered recent or current evolutionary divergences within these
148 taxonomic lineages.

149

150 Remigial replacement during preformative moults is likewise fixed, following the same
151 sequences described above for prebasic moults, despite varying nodal positions among
152 primaries and a proximal wave from S1 appearing to be suppressed in many passerines
153 exhibiting eccentric moults (Pyle 1997, Gargallo 2013, Jenni and Winkler 2020). In these
154 and other species exhibiting partial but not eccentric preformative moults, distal
155 replacement from a node at the second tertial appears to be prioritized among
156 secondaries, with for example S6 through S4 being replaced distally and at decreasing
157 rates of frequency (Pyle 1997, Gargallo 2013); replacement extent during eccentric
158 moults has been correlated with hatching date within the breeding season (Elrod et al.
159 2011).

160

161 Among upperwing secondary coverts, feathers are generally replaced in a distal direction
162 among each tract (marginal, median, and greater coverts) during preformative moults, as
163 implied by most resultant moult phenologies (Guallar and Jovani 2020a, 2020b),
164 whereby most or all formative feathers are located proximal to most or all juvenile
165 feathers, defining moult limits following partial replacement (Pyle 1997, Jenni and
166 Winkler 2020). Although exceptions and some variation in covert-replacement
167 phenologies can occur between and occasionally within species (Pyle 1997, Guallar et al.
168 2014, Guallar and Jovani 2020b, Jenni and Winkler 2020), in most cases a prevailing
169 order to feather replacement appears to be maintained. Prealternate moults may involve
170 different replacement mechanisms, as feather-replacement sequences can vary to a
171 greater extent than those of prebasic and preformative moults, e.g., among the
172 secondaries of gulls (Pyle et al. 2018b) and the resultant wing-covert phenologies of
173 passerines (Guallar and Jovani 2020a, 2020b; Jenni and Winkler 2020). In most cases,
174 however, replacement of coverts is less extensive during prealternate than during
175 preformative moults and the sequences of each can be identified (see examples in Figures
176 1 and 2 and Table 1, and discussion of exceptions to this pattern below). Among prebasic
177 and preformative moults within species, by contrast, sequence is relatively fixed among
178 broader evolutionary lineages, and may be controlled by neurological as opposed to
179 hormonal mechanisms within restorative processes that include moult (Pyle 2013).

180

181 As, such, I propose defining moults that take place partially or entirely on non-breeding
182 grounds on the basis of evolutionarily fixed feather-replacement sequences as opposed to
183 highly plastic timing or location of replacement. Sequential feather replacement can be

184 suspended for migrations and protracted throughout nonbreeding periods, leading to
185 strategies in which partial (prealternate) body-feather and wing-covert moults,
186 commencing a new sequence, can overlap the completion of protracted flight-feather and
187 wing-covert moults.

188

189 For example, in the well-studied Western Kingbird *Tyrannus verticalis*, moult of
190 primaries in both first-year birds and adults can variably commence on breeding grounds,
191 occur partially or entirely at stopover locations, and/or suspend to complete as late as
192 spring on winter grounds, with a second partial replacement of feathers occurring on the
193 winter grounds in spring (Pyle 1997, Rohwer 2008, Barry et al. 2009). Under the
194 sequence-based definition proposed here, the entirety of remigial replacement, despite
195 where it occurs, is considered part of the prebasic or preformative moult, with an
196 overlapping prealternate moult in spring that includes a renewed sequence of replacement
197 among body feathers, inner greater coverts, and tertials (Figure 1). Eccentric preformative
198 moult of primaries usually completes starting from a predetermined node (Gargallo 2013)
199 and thus should be considered a single moulting episode as opposed to two separate
200 episodes, as previously interpreted by Pyle (1997).

201

202 Due to gradual temporal shifts in plumage colouration during protracted moults, first-year
203 male Summer Tanagers *Piranga rubra* present a good example for defining first-cycle
204 moults based upon sequence among upperwing coverts and tertials. Adult males in
205 definitive basic and definitive alternate plumages exhibit uniformly red feathers whereas
206 in first-cycle males, feather colour appears to track timing of replacement, juvenile

207 feathers being dull yellow, formative feathers replaced in late summer and early fall
208 being brighter yellow, and feathers replaced on winter grounds varying from orange-
209 yellow in late fall to red in spring (Figure 2). Although feather colour should not be used
210 to define moults (Howell et al. 2003, Howell 2010), the progression of the partial
211 preformative and prealternate moults in first-year male Summer Tanagers can be
212 assumed according to the extent of redness in feather colouration (cf. Figure 22 in Howell
213 2010:17), and indicates that this moult can occur throughout the non-breeding period and
214 overlap a prealternate moult in spring (Figure 2, Table 1A). Moult of brown and blue
215 wing feathers can similarly be traced with first-year male Indigo Buntings *Passerina*
216 *cyanea* (Table 1B). In both the kingbird and tanager examples, first prealternate moults
217 can be elucidated and, as expected, are found to be similar in extent to that of adults in
218 passerines (Pyle 1997).

219

220 **CLEARING UP PREVIOUS INTERPRETATIONS**

221

222 Taking a sequence-based definition of moults has the potential to clear up previously
223 confused terminologies in species among the Red-backed Shrike complex (Pyle et al.
224 2015) and Yellow-bellied Flycatcher (Carnes et al. 2021), allowing for direct comparison
225 of moults among these genera. Among European species treated by Jenni and Winkler
226 (2020), moulting episodes can also be clarified. Barred Warblers, for example, can be
227 considered to undergo a complete prebasic (postbreeding) moult and an incomplete
228 eccentric preformative (postjuvenile) moult, each of which concludes with secondaries on
229 winter grounds; this interpretation may help confirm suspicions that eccentric moults are

230 confined to the first cycle. The "additional prebreeding moult" reported to include wing
231 coverts, tertials, and rectrices, would be considered a new moulting sequence involving
232 the prealternate (prebreeding) moult which, in some individuals, overlaps the conclusion
233 of the suspended moults. Similarly, for first-year Western Yellow Wagtails *Motacilla*
234 *flava* the "first phase" of the prebreeding moult would be considered part of a suspended
235 preformative moult while the "second phase" of the prebreeding moult would be
236 considered the prealternate moult in both first-year and adult birds, as defined by a
237 renewed sequence in feather replacement. If a third replacement of body feathers occurs
238 in this species, as sometimes reported but may not be fully documented at the individual
239 level (Cramp 1992), a presupplemental moult would be identified under H-P terminology,
240 and its placement would depend on when it evolved along ancestral lineages. In Figure
241 564 of Jenni and Winkler (2020), greater coverts 4-5 could be formative and greater
242 coverts 6-10 juvenile, rather than all being a single generation (prebreeding). All
243 populations of Common Whitethroats would undergo complete prebasic and partial
244 (occasionally eccentric) preformative moults which, as in *Lanius* shrikes (Pyle et al.
245 2015), can vary as to geographic location and extent prior to suspension for southbound
246 migration. Potential extra inserted prealternate moults on winter grounds (e.g., in Figures
247 313-320 of Jenni and Winkler 2020) can also be detected, and variation in moult
248 strategies in Common Whitethroats can be compared in an evolutionary sense. Inserted
249 prealternate moults can similarly be identified in other species with moult categories 3-5
250 of Jenni and Winkler (2020:34-38, 72-74) including, for example, the *Curruca* warblers
251 illustrated in Figure 57, which appear to have undergone eccentric preformative moults
252 and have first alternate tertials (S8-S9) and inner greater coverts.

253

254 In many species, a sequence-based definition results in the prealternate moult being
255 defined as simply including those feathers moulted for a second time within the first
256 moult cycle; i.e., replacing either formative or basic with alternate feathers, but this does
257 not form the basis of definition. In some species the first prealternate moult can be more
258 extensive than the preformative moult, for example in Willow Warbler *Phylloscopus*
259 *trochilus*, Indigo Bunting, American Yellow Warbler *Setophaga petechia*, and Bobolink
260 *Dolichonyx oryzivorus* (Pyle 1997, Wolfe and Pyle 2011, Jenni and Winkler 2020),
261 resulting in juvenile wing feathers being replaced by first alternate feathers. In these
262 species definitive prealternate moults are also extensive, first prealternate moults often
263 proceed in the same sequence as the preformative moults, and a sequence-based
264 definition for each moult is maintained, despite variability in the sequence of some (but
265 not all) prealternate moults, as mentioned above. Many other species reported to have
266 more extensive prebreeding than postjuvenile moults (Jenni and Winkler 2020) would be
267 interpreted under a sequence-based system as having suspended preformative moults.

268

269 A sequence-based definition can also be applied to non-passerine species that moult twice
270 away from breeding grounds, such as those among divers, skuas, terns, and waders. Many
271 species in these and other non-passerine families have well-documented overlapping
272 prebasic and prealternate moults or, for example among terns and waders, overlapping
273 prealternate and presupplemental moults (Pyle 2008, 2019), in each case feather-
274 replacement sequence defines the initiation of each moult. It is thus not surprising that
275 passerines can also show overlapping moults. Large non-passerine species that exhibit

276 Staffealmauser or stepwise moults are generally considered to have incomplete prebasic
277 moulting episodes as opposed to overlapping moults (Pyle 2005, 2008), although in some
278 species (e.g., among Sulidae and Cathartidae) with rather continuous flight-feather
279 replacement during prebreeding years, overlapping prebasic moults may also be inferred
280 using a sequence-based approach (Pyle 2008, Chandler et al. 2010).

281

282 **CONCLUSIONS**

283

284 I can think of no examples in which a sequence-based definition cannot be effectively
285 applied to moult in migratory bird species. Although more study is needed on actual
286 feather replacement sequence vs. resulting phonologies following partial moults
287 (especially among wing coverts), I believe a sequence-based approach will eventually
288 enable a clearer interpretation of moult strategies, especially when using an evolutionary
289 approach to the definition of moults. Additionally, although some minor exceptions or
290 perplexing situations might be predicted, solutions can be identified if definitions are
291 based on the evolutionary histories of moult strategies. Due to the different bases for
292 definition, moult terms under the life-history and H-P terminologies should not be
293 considered synonyms of each other; however, should life-history definitions of
294 postjuvenile, postbreeding, and prebreeding moults adopt a similar sequence-based
295 approach to that described using H-P terminology here, moults away from breeding areas
296 could be substantially clarified. In any case, those examining adaptive evolutionary
297 factors that affect moult strategies should carefully define preformative/postjuvenile,
298 prebasic/postbreeding, and prealternate/prebreeding moults. For such analyses I

299 recommend using the sequence-based approach proposed here (cf. Guallar et al. 2021),
300 while separate analyses considering feather replacement both pre- and post-migration (cf.
301 Hall and Tullberg 2004, Delhey et al. 2020) may shed further light not only on
302 environmental and life-history factors affecting the extents of moults overall, but on the
303 those affecting variation in extents prior to suspension, at both individual and species
304 levels.

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465 Table 1. Examples of sequence-based definitions following the preformative and first prealternate moults in first-year male Summer
 466 Tanagers *Piranga rubra* and Indigo Buntings *Passerina cyanea*. Links are to images catalogued by the Cornell Lab of Ornithology's
 467 Macaulay Library. Feather-tract definitions, feather numbering, and abbreviations for marginal coverts (MaC), median coverts (MeC),
 468 greater coverts (GC), carpal covert (CC), alula (A), secondaries (S), and primaries (P) follow those of Figure 9 in Jenni and Winkler
 469 (2020:10); rectrices (RR) are numbered proximally on each side of tail. Designations are proposed for illustration of a sequence-based
 470 approach and, in some cases may be ambiguous, approximate, or not listed if feathers are not entirely diagnosable.
 471

Macaulay #	Formative Summer	Formative Fall/Winter	Formative Spring	First Alternate Spring
A. Summer Tanager				
ML62817821 ¹	MaC, GC8-9, A1-2	MeC, GC1-7, 10		
ML157088011	MeC1-3, A1-2	MeC4-8, GC1-8	S8-9, RR	GC9-10
ML233637131	MaC, MeC, GC2-7, A1-2		GC1, S8-9, RR	MaC, MeC6, GC8-10
ML55755651	some MaC, MeC1-4, A1	GC1-5, CC, A2, R5-6	S8-9 ² , R3-6	some MaC, MeC5-8, GC6-10, R1-2
ML153839791	Mec8, A1		S8-9 ³ , P1-2 ³ , RR	MaC, MeC, GC, RR
B. Indigo Bunting				
ML51314551	GC6-7, S8-9	GC1-5, S5-6, P5-9, RR	A2-3	Mac, MeC, GC7-10
ML236845401	MeC8, GC1, 3; S7-9	A2-3, P6-9, RR		MaC; MeC; GC2, 4-10
ML94449631	GC4-5, S8	P5-9, S9, RR	some MaC, GC1-3, CC, S7	MaC, MeC, GC6-10
ML59025811	some MaC; GC1, 9-10; S9	GC7-8, S7, P4-9, R2-6	S4-6	Mac, MeC, GC2-6, S8, R1
ML157869921	GC1-3, 10; MeC5, S7,9, R3-6	S4-6, A2-3, P5-9		MaC, MeC, GC4-9, S8, R1-2

472
 473 ¹Image taken in December; remaining images taken during 14 April-19 May.
 474 ²S8 may be alternate
 475 ³Adventitious or anomalous preformative replacement pattern for this species

Figure Legends

Figure 1. Progression of preformative, prebasic, and prealternate moults away from breeding grounds in Western Kingbird (*Tyrannus verticalis*); see Table 1 for feather numbering. (A) Formative feathers (pale gray) replaced in late summer on moulting grounds include inner greater coverts, S8-9, and P6-7, before suspending eccentric moult for migration to winter grounds; remaining feathers are juvenile (tan). (B) Similar to (A) but preformative moult had continued on winter grounds with outer greater coverts, S6-7, and P6-8 (dark gray) in fall and winter, and with S5-4 and P9-10 in spring (black), overlapping first prealternate moult of inner three greater coverts and S8 in timing (also black). (C) Adult in summer following definitive prebasic and prealternate moults: basic secondary coverts, S7-9 and P1-5 along with corresponding primary coverts were replaced in late summer on moulting grounds, followed by suspension for migration, replacement of S1-3 and P6-8 in fall and winter, and replacement of S4-6 and P9-10 and corresponding primary coverts in spring (black) overlapping prealternate moult of inner greater coverts and S8-9 in timing (also black). Wings based on specimens at the California Academy of Sciences (CAS): (A) CAS63960, Guerrero, Mexico, 7 November 1950; (B) CAS 88236, California, 28 May 1965; (C) CAS46917, California, 12 June 1898. See also Figure 172 in Pyle (1997) for more information and see [PSM17928](#) at Slater Museum of Natural History (2021) for an example with moult patterns similar to (C).

Figure 2. Progression of preformative and first-prealternate moults in first-year male Summer Tanagers (*Piranga rubra*) as based on specimens at the California Academy of Sciences (CAS). Primaries, primary coverts, and most secondaries remain as juvenile feathers (tan) until the second prebasic moult. **(A)** Formative feathers were replaced on or near summer grounds (yellow) followed by suspension for migration and continued replacement of formative feathers in late fall or early winter on winter grounds (CAS32863, Panama, 10 December 1929). **(B)** Most formative secondary coverts and S8 were replaced on or near summer grounds (yellow), followed by formative carpal covert and S9 replaced in fall or winter (orange) and first prealternate body feathers (see below) and marginal coverts (red), replaced in spring (CAS80003, Arizona, 19 June 1893). **(C)** Similar to **(B)** but both S7 and S9 were replaced in spring (red) and some median and greater coverts and S8 are first alternate, also red and replaced in spring; the S8 was presumed also replaced during the preformative moult (CAS29736, Arizona, 16 June 1927). **(D)** Similar to **(C)** but S6 was replaced at the end of the preformative moult in spring, overlapping the first prealternate moult that included a greater number of wing coverts and S8-9 (CAS53100, Georgia, 26 April 1907). **(E and F)** The above four specimens (left-to-right), ventral and dorsal aspects, respectively, showing formative (yellow, orange, and red) and first alternate (red) body feathers with feather colour generally reflecting replacement locations and timing (cf. Figure 22 in Howell 2010:17). The left two individuals had retained all juvenile rectrices whereas the right two birds had formative rectrices that were replaced in late winter or spring. Undertail coverts and uppertail coverts were often orange, indicating retention of juvenile feathers in this tract

over fall migration. See Table 1 for feather numbering and more examples of first-cycle males.

Figure 1.

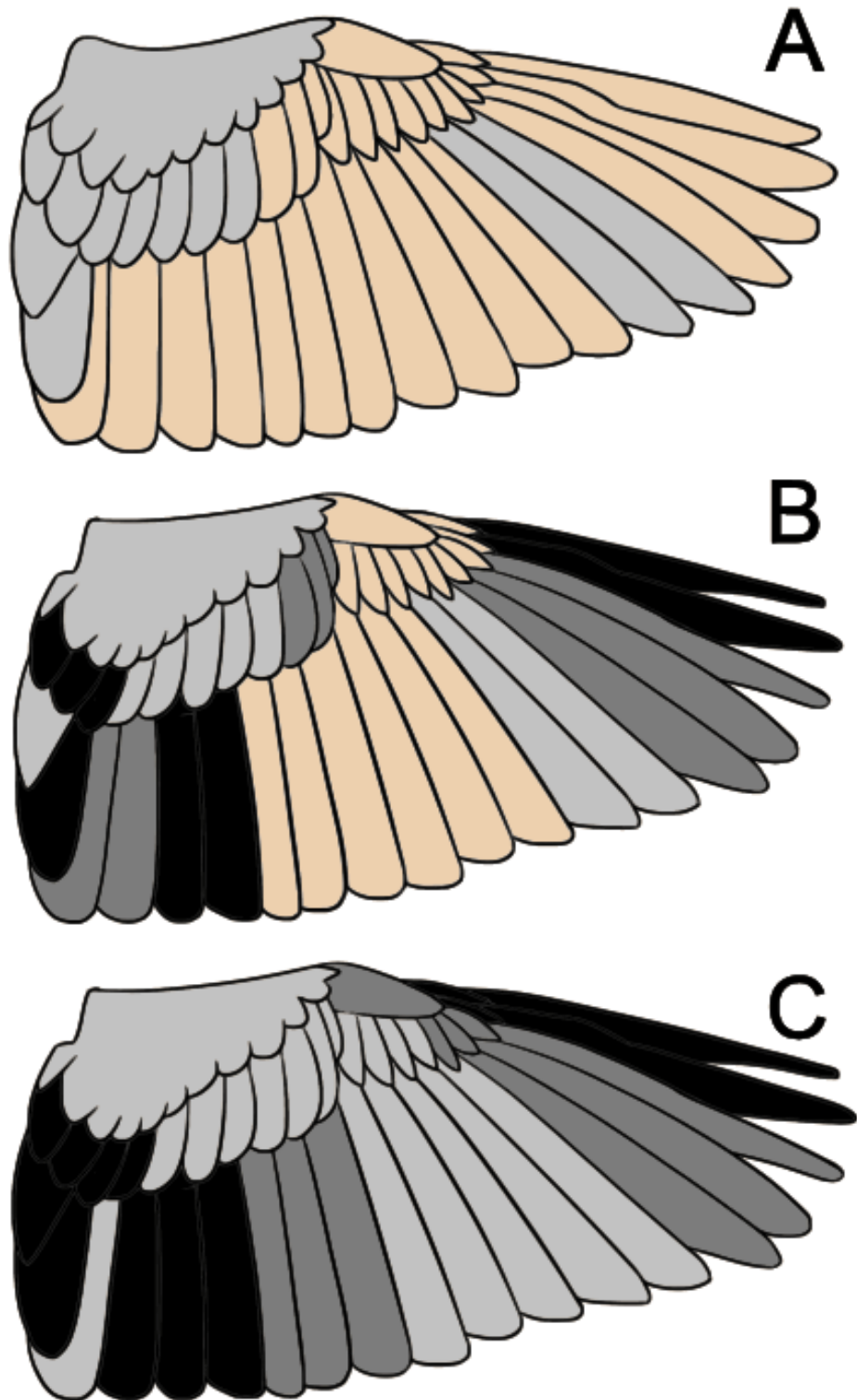


Figure 2.

