Molting strategies of sapsuckers (*Sphyrapicus*): Effects of migration distance and age through the fourth and later plumage cycles

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ABSTRACT—Woodpeckers have unique molting patterns in which primaries and rectrices are replaced during all molt cycles but primary coverts and secondaries can be retained during prebasic molts. Details concerning replacement sequences and extents, however, are poorly known. We investigated molt patterns in 5 sapsucker (*Sphyrapicus*) taxa through the examination of 675 museum specimens and additional analysis of digital images. Sapsuckers replace fewer feathers per molt than most other North American woodpeckers. All individuals in 3rd basic plumage (3rd/4th calendar years) and a proportion of sapsuckers in 4th basic plumage (4th/5th calendar years) can retain juvenile feathers and be aged, a novel finding among woodpeckers and most bird species with the exception of some owls and larger flighted birds. Primary coverts and secondaries are replaced convergently from the outsides of each feather tract and Staffelmauser-like molting patterns can ensue. Asynchronous replacement of primary coverts and primaries (which are replaced distally) is unique to woodpeckers and kingfishers and may indicate that it evolved prior to the split of Piciformes and Coraciiformes. Juvenile body feathering and secondary coverts are retained longer into the fall and winter in the more highly migratory Yellow-bellied (*S. varius*) and Red-naped (*S. nuchalis*) sapsuckers, adding crypsis for migration and due to time constraints for molting. The extent of prebasic molts correlated positively with migration distance, being greater in Yellow-bellied and Williamson's (*S. thyroides*) sapsuckers and lowest in the nearly resident nominate subspecies of Red-breasted Sapsucker (*S. ruber ruber*), perhaps as related to the effects of solar exposure on an annual basis. Modeling of age structure through the 3rd and later basic plumages can inform conservation management related to salvage logging, climate-affected burn regimes, and the restoration of more favorable habitats. *Received 20 April 2023. Accepted 28 November 2023.*

Key words: age-determination, ecology, evolution, kingfisher, molt, woodpecker.

Estrategias de muda de chupasavias (Sphyrapicus): efectos de la distancia de migración y de la edad durante el cuarto y último ciclos de plumaje

RESUMEN (Spanish)—Los carpinteros tienen patrones de muda únicos, en los que las primarias y las rémiges son reemplazadas durante todos los ciclos de muda pero las coberteras primarias y secundarias pueden ser retenidas durante las mudas prebásicas. Sin embargo, no se tiene mucho conocimiento de los detalles de las secuencias de reemplazo y extensiones. Investigamos patrones de muda de 5 taxa de chupasavias (*Sphyrapicus*) examinando 675 especímenes de museo y analizando imágenes digitales adicionales. Los chupasavias reemplazan menos plumas por muda que la mayoría de los carpinteros norteamericanos. Todos los individuos en su plumaje básico 3rio (3ro/4to año calendario) y una proporción de los chupasavias en su plumaje básico 4rio (4to/5to año calendario) pueden retener plumas juveniles y ser de edad, un hallazgo nuevo entre los carpinteros y entre la mayoría de especies de aves, con la excepción de algunas lechuzas y aves voladoras de gran tamaño. Las coberteras primarias y secundarias son reemplazadas convergentemente a partir del exterior de cada canal de plumas, que a veces puede ser seguido de un patrón de muda tipo Staffelmauser. Un reemplazo asincrónico de coberteras

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primarias y de primarias (las cuales son reemplazadas distalmente) es único de carpinteros y martines pescadores y podría indicar que evolucionó previo a la separación de Piciformes y Coraciiformes. El plumaje corporal juvenil y las coberteras secundarias son retenidos durante más tiempo entrados el otoño e invierno en las especies de chupasavias más altamente migratorias *Sphyrapicus varius* y *S. nuchalis*, sumando camuflaje a la migración y debido a restricciones temporales para la muda. La extensión de las mudas prebásicas tuvo una correlación positiva con la distancia de migración, mayor en los chupasavias *S. varius* y *S. thyroides* y menor en la subespecie *S. ruber ruber* que es prácticamente residente, posiblemente relacionado a efectos de la exposición solar anual. El modelado de la estructura etaria utilizando el plumaje 3rio y plumajes básicos posteriores puede ayudar a tomar decisiones de manejo de conservación relacionadas con tala de rescate de maderas, regímenes de quemas afectados por el cambio climático y restauración de hábitats más favorables.

Palabras clave: carpintero, determinación de edad, ecología, evolución, martín pescador, muda.

Woodpeckers have unique molting patterns among birds whereby body feathers, primaries, and rectrices are replaced in most species but primary coverts and secondaries can be retained during preformative and annual prebasic molts (Pyle and Howell 1995, Pyle 2022a). During the preformative molt, which takes place during the 1st molt cycle, all visible juvenile primary coverts are retained, as well as most or all secondaries and usually some distal upperwing secondary coverts. During the 2nd prebasic molt (at approximately 1 year of age), 4 to all visible juvenile primary coverts and up to 6 juvenile secondaries can be retained for a 2nd year, and during the 3rd prebasic molt (at 2 years of age), up to 2 juvenile primary coverts and 2 juvenile secondaries can continue to be retained for a 3rd year, allowing determination of birds in their 2nd and 3rd molt cycles or 2nd through 4th calendar years (Siegel et al. 2016, Pyle 2022a). With a few exceptions, these molt extents and replacement patterns appear to occur throughout all woodpecker genera, as well as in wrynecks (Laesser and van Wijk 2018), but not in other families within Piciformes (Pyle, 2023, unpubl. data).

In woodpeckers, the sequence of replacement among secondaries appears to be bilateral from the middle tertial and proximal from the outermost secondary, and primary coverts may be replaced convergently from each end of the tract, differing from the distal replacement of primaries (Pyle 2022a). These sequences need to be confirmed, however, as well as variation in extents for each prebasic molt. It is possible, for example, that these feathers are replaced in a pattern resembling Staffelmauser (or stepwise molt) in larger birds (Stresemann and Stresemann 1966), whereby molt within each tract continues in sequence from the point it arrested the previous year, while at the same time initiating new replacement sequences, resulting in multiple active molt waves and "sets" of replaced feathers (Pyle 2006). However, such molting patterns have not been documented in woodpeckers.

Determining the age of captured birds is critical to demographic analyses on population structure, which can help to identify effective population size, recruitment rates, and survival and dispersal patterns, and thus used to guide conservation and habitat management actions. Such age-determination for demographic analyses, leading to conservation and habitat management actions, is a primary focus of programs such as the Monitoring Avian Productivity and Survival (MAPS) and Monitoreo de Sobrevivencia Invernal (MoSI) programs (DeSante et al. 2015, Albert et al. 2020). In woodpeckers, specifically, modeling of age structure through the 3rd plumage cycle in Black-backed Woodpeckers (*Picoides arcticus*) indicated that natal dispersal of 1st-cycle birds is the primary means by which this species colonizes recently burned areas in western North American forests, whereas breeding dispersal of adults is uncommon (Siegel et al. 2016). More generally, recent studies have found significant correlations between yearling proportion and habitat-structure covariates for landbirds breeding in the North American boreal region (Pyle et al. 2020). Delineating precise sequences and extents among the annual molts of woodpeckers can help determine age structure within populations, which in turn can inform conservation management decisions related to salvage logging and habitat restoration (Siegel et al. 2016, Pyle et al. 2020).

In addition to helping with age determination and demographic analyses, studies of molt can provide insight into the evolution and natural history of an avian species. Migration extent, climate, flight mechanics, feeding behaviors, and reproductive timing all have the potential to influence molt characteristics. For example, highly migratory species can suspend molts over migration and complete them during a protracted period on molting or

Table 1. Number of specimens examined per plumage class in 5 taxa of sapsuckers: Yellow-bellied Sapsucker (*Sphyrapicus varius*), Red-naped Sapsucker (*S. nuchalis*), the 2 subspecies of Red-breasted Sapsucker (*S. ruber ruber* and *S. ruber daggettii*), and Williamson's Sapsucker (*S. thyroides*). See text for a further breakdown of specimens considered in juvenile plumage, undergoing preformative molt, and in formative plumage.

Plumage	S. varius	S. nuchalis	S. r. ruber	S.r. daggetti	S. thyroides
Juvenile/Formative	56	55	32	99	49
Second Basic	19	23	24	35	19
Third Basic	8	10	9	17	8
Fourth Basic	5	4	5	3	6
Definitive Basic	42	21	24	57	45
Total Sampled	**130**	**113**	**94**	**211**	**127**

wintering grounds, whereas resident, higher-latitude species may undergo quicker and less-complete molts on or near breeding grounds due to the constraints of the oncoming winter (Pyle 1998, 2008, 2022b; Pyle et al. 2009, 2018; Kiat et al. 2019; Terrill et al. 2020). Variation in the extent of the molts may also be related to time and energy constraints imposed upon molt as related to climate, date of hatching, and other factors (Delhey et al. 2020; Pyle 2022a, 2022b).

The 4 species of sapsuckers (*Sphyrapicus*) appear to replace fewer primary coverts and secondaries on average during prebasic molts than other North American woodpeckers (Pyle and Howell 1995, Pyle 2022a). Sapsuckers also exhibit variable migration strategies. The Yellow-bellied Sapsucker (*S. varius*) is a long-distance migrant breeding in boreal regions of North America and wintering in the southeastern United States through the Caribbean and Central America (Walters et al. 2020a); the Red-naped Sapsucker (*S. nuchalis*) is a medium-distance migrant, breeding in interior western regions of southern Canada and the northern United States and wintering in the southwestern United States through central Mexico (Walters et al. 2020b); the Red-breasted Sapsucker (*S. ruber*) breeds in coastal regions of the Pacific Northwest and is a resident or short-distant migrant, with the northern subspecies (*S. r. ruber*) tending to be more resident than the southern subspecies (*S. r. daggetti*; Walters et al. 2020c); and the Williamson's Sapsucker (*S. thyroides*) breeds at high elevations in the Cascade and Sierra Nevada mountain ranges of North America and can be resident or show down-slope migrations (Gyug et al. 2020). Here we investigate and describe molt patterns in these 5 *Sphyrapicus* sapsucker taxa.

We clarify details of replacement sequences and extents during the preformative and prebasic molts, relate these to age determination, and test the hypotheses that molts are affected by the differing migration strategies among these 5 taxa. We anticipate that our results will lead to improved conservation management of each taxon.

Methods

Specimen examination and plumage categorization

Pyle examined specimens of sapsuckers located at the California Academy of Sciences (CAS), San Francisco, and the Museum of Vertebrate Zoology (MVZ), Berkeley, California. Each specimen was identified to species and subspecies based on information on the specimen labels and as confirmed with criteria listed in Pyle (2022a). Hybrids or suspected hybrids between species were excluded. Each individual was categorized to plumage cycle (age) and molt status according to the "WRP" cycle-based age-coding system (Wolfe et al. 2010, Pyle et al. 2022). Plumage categories included 1st cycle (FCJ/FPF/FCF, corresponding to hatching/2nd-year or "HY/SY" under calendar-year age coding; Pyle 2022a), 2nd basic plumage (SCB, corresponding to 2nd/3rd calendar year or "SY/TY"), 3rd basic plumage (TCB corresponding to 3rd/4th calendar year or "TY/4Y"), 4th basic plumage (4CB corresponding to 4th/5th calendar year or "4Y/5Y"), and definitive basic (DCB, corresponding to after 2nd/3rd calendar year or "ASY/ATY" according to Pyle 2022a). Specimens categorized as in their 1st cycle, including juvenile plumage (FCJ), undergoing preformative molt (FPF), and formative plumage
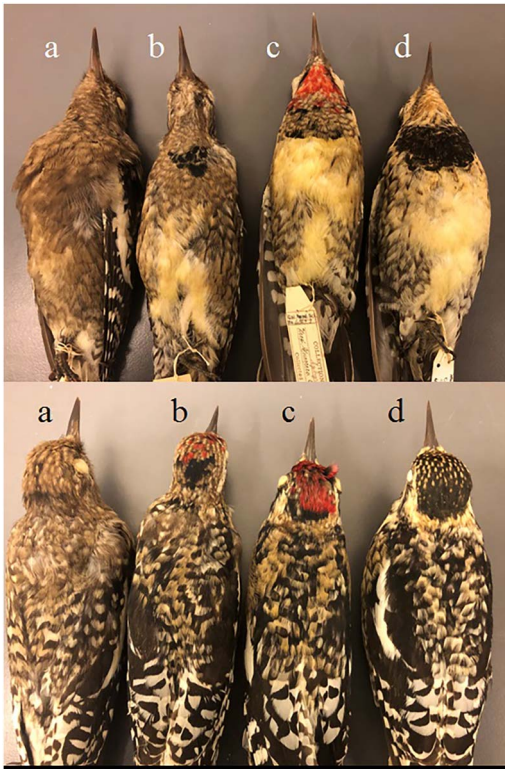
Figure 1. Yellow-bellied Sapsuckers (*Sphyrapicus varius*) collected during their 1st cycle, in juvenile plumage (a), undergoing preformative molt (b–c), and in formative plumage (d; not undergoing active molt), showing differing proportions of remaining juvenile body feathers into winter and spring. These were scored as 100% juvenile feathering (a), 90% (b), 35% (c), and 5% (d). Specimens: CAS 24548, Manitoba, Canada, 6 September 1921 (a); CAS 71957, Oaxaca, Mexico, 14 November 1964 (b); CAS 63849, Guerrero, Mexico, 13 November 1951 (c); CAS 45360, Wisconsin, USA, 6 June 1889 (d).

(FCF), were combined for analysis because it was unknown whether or not the preformative molt may have suspended or had completed by the date of collection. For categories other than 1st cycle, specimens undergoing active replacement of primaries when collected were excluded, as were individuals in which age determination was uncertain. All sapsucker specimens at CAS were examined and additional specimens at MVZ were subsequently examined, with the goal of sampling at least 20 individuals per taxon/plumage group (achieved for 14 of 25 categories; Table 1). To attempt reducing biases due to location or time of specimen collection, specimens of given plumages were randomly selected among the trays at MVZ.

For further reference, Pyle also examined photographs of Yellow-bellied Sapsucker wings taken as part of the Boreal Monitoring Avian Productivity and Survival (MAPS) Program located in northeastern Alberta, Canada, during the summers of 2011–2023. These photographs were taken in order to age individuals and determine age structure within this population (Foster et al. 2017, Pyle et al. 2020). All birds were banded, allowing determination of recaptures between years.

For each specimen, feathers by generation were categorized and feather replacement patterns were analyzed, with the goal of describing the extent and sequence of each molt. For birds collected during the 1st cycle, the proportion of unmolted juvenile body feathers that remained was estimated to the nearest 5% (Fig. 1, Supplemental Fig. S1). During late summer and fall, caution was exercised not to confuse juvenile with freshly molted basic feathers, which can be fringed with buff or brown and resemble juvenile feathers (Pyle 2022a). Within alar tracts, each upperwing median and greater secondary covert (12 each) was scored as either juvenile or formative. A composite molt score for each specimen was calculated as the number of feathers that had been replaced (formative) among the outer 9 median coverts and inner 8 greater coverts (score range 0–17), representing feathers found to either have been replaced or retained among the sample of 1st-cycle birds.

For the prebasic molts, each of the 6 outer primary coverts and all 10 secondaries were scored as either juvenile, newly replaced basic, or older basic, as based on shape and extent of wear (see Pyle 2022a). For birds identified as in 4th basic plumage (4CB), older basic feathers were further categorized as "1 yr old" (replaced at the 3rd prebasic molt) or "2 yrs old" (replaced at the 2nd prebasic molt). An attempt was also made to similarly classify older basic feathers of definitive basic plumage (DCB) but lack of confidence in determining molt generation for every feather precluded accurate categorization and analysis. Molt sequences were inferred by wear clines (Pyle 2022a): newer feathers adjacent to more worn feathers indicate the sequence in which feathers were replaced due to time lags between each feather, while larger contrasts indicate a time lag between annual molts (Pyle 2005, 2013, 2022a; Rohwer and Rohwer 2018).

Secondaries were numbered from outermost (s1) to innermost (s10). Primary coverts were numbered from innermost (pc1) to outermost (pc10), corresponding to

primary numbering (see Supplemental Fig. S2a). The inner 4 primary coverts (pc1–pc4) could not be accurately assessed without damaging the specimens, and thus were not scored. For each specimen, a composite score for the number of secondaries and primary coverts that were newly replaced basic feathers was calculated (range 0–16).

Statistical analyses

To examine the relationship between molt and time of year for all taxa, Schofield used multiple linear regression models with the response variables of (1) percent juvenile body feathers retained, and (2) the number of primary coverts and secondary feathers replaced (mean composite molt score) in individuals in their 2nd and later basic plumages (i.e., birds past their first molt cycle). We examined the explanatory variables of month and taxon, along with interactions thereof.

We considered month to be a continuous variable because molt initiates at a consistent time of the year for all species. When examining juvenile feather retention, we considered July as the first month because it is when juvenile sapsuckers of all species can begin body molt. When examining mean composite molt score, we considered November as the first month, because covert replacement in all taxa can be completed by October. Because Yellow-bellied Sapsuckers have several distinct molt characteristics, we also created a separate linear model to examine the difference in trends between juvenile feather retention in this species alone and in all other sapsucker taxa combined. Similarly, to investigate how a bird's age relates to molt extent, we used a multiple linear regression model to examine the relationship between mean composite molt score and molt cycle, with mean composite molt score as the response variable and molt cycle as the explanatory variable.

For all models we used a Kolmogorov-Smirnov (K-S) test of normality using the function *ols_test_normality()* in the R package *olsrr* to verify that linear models met the assumption that model residuals were normally distributed. Where overall model results were significant, we calculated the least squared means (LSM) of the model trends for each taxon using the *lstrends* function in the R package *lsmeans*. We then conducted pairwise comparisons of the LSMs to examine whether the trends differed
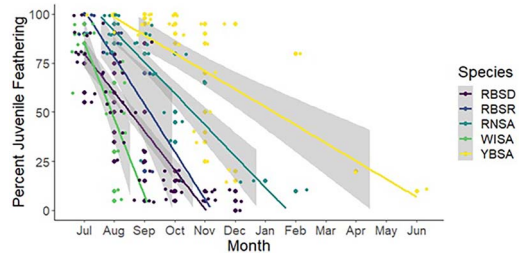
Figure 2. Percentage of juvenile feathers remaining by month of collection in specimens of 5 sapsucker taxa: Yellow-bellied (*Sphyrapicus varius*; YBSA), Red-naped (*S. nuchalis*; RNSA), northern Red-breasted (*S. ruber ruber*; RBSR), southern Red-breasted (*S. ruber daggetti*; RBSD), and Williamson's (*S. thyroides*; WISA) sapsucker. July, when juvenile feather replacement starts in all sapsucker taxa, is considered the first month in this analysis. Envelopes represent 95% confidence intervals. Migration occurs in these species primarily during October. Points are randomly jittered on the *x*-axis to help visualize sample size.

between taxa. To account for multiple comparisons, a Bonferroni correction was used to adjust *P* values.

Results

Overall, 675 specimens were scored, with sample sizes ranging from 94 *ruber* Red-breasted Sapsuckers to 211 *daggetti* Red-breasted Sapsuckers (Table 1). Of these, 291 were categorized as in the 1st cycle (FCJ, FPF, or FCF), 120 as in 2nd basic plumage (SCB), 52 as in 3rd basic plumage (TCB), 23 as in 4th basic plumage (4CB), and 189 as in definitive basic plumage (DCB). The 1st-cycle birds included those in complete juvenile plumage (32 specimens), those with formative and juvenile body feathers remaining (137 specimens), and those without juvenile body feathers remaining (122 specimens).

Timing of the preformative molt

The 169 1st-cycle birds examined that were in juvenile plumage or had retained juvenile feathers (a subset of the 1st-cycle category in Table 1) included 36 Yellow-bellied Sapsuckers, 38 Red-naped Sapsuckers, 11 *ruber* Red-breasted Sapsuckers, 63 *daggettii* Red-breasted Sapsuckers, and 21 Williamson's Sapsuckers. Yellow-bellied Sapsucker differed from the other 4 taxa in that juvenile body feathers could remain through winter and, in some cases, through the 1st breeding season (Fig. 1–2). The number of months including
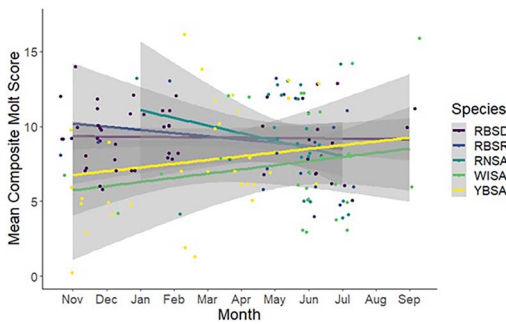
Figure 3. Mean composite secondary covert replacement score (range 0–16) by month of collection in 5 sapsucker taxa. November is considered as the first month as secondary covert feather replacement is completed in October for all taxa except Yellow-bellied Sapsucker. See Figure 2 for species taxon codes. Points are randomly jittered on the *x*-axis to help visualize sample size.

individuals with retained juvenile feathers ranged from 2 in Williamson's Sapsuckers (Jul and Aug) to all 12 in Yellow-bellied Sapsucker. In Yellow-bellied Sapsucker, our results suggest that the preformative molt can continue through March or April (Fig. 1); juvenile feathers remained on all 14 specimens collected in December–March (100%) but only 3 of 13 specimens collected in April–June (23%). Among the remaining 4 taxa, the preformative molt of body feathers appeared to complete by the end of September in Williamson's Sapsucker, the end of October in Red-breasted Sapsucker (both subspecies), and the end of January in Red-naped Sapsucker (Fig. 2).

Linear models indicate there was a significant negative relationship between percent juvenile feathering retained and month, taxa, and interactions thereof ($F_{9,159} = 49.83$, $P < 0.001$, Adj. $R^2 = 0.723$), with the assumption of normality of residuals met (KS test $D = 0.08$, $P = 0.223$). LSMs show that monthly trends in the percent of juvenile feathers retained was consistently negative but varied, ranging from -39.13% per month ($\pm 7.88\%$ SE) in Williamson's Sapsucker to -9.15% per month ($\pm 1.27\%$ SE) in Yellow-bellied Sapsucker (Supplemental Table S1). Pairwise comparisons of the LSMs indicate that the differences in these trends were significant between multiple taxa (Supplemental Table S2, Fig. 2). Most notably, there were significant differences in the rate of juvenile feather replacement between Yellow-bellied Sapsucker and all other individual taxa except *ruber* Red-breasted

Sapsucker, potentially an artifact of low sample size for *ruber* ($n = 11$). The monthly decline in percent juvenile feathering of Yellow-bellied Sapsucker alone (-9.15 ± 1.63) differed significantly from that of the other 4 taxa combined (-17.28 ± 1.42; $t = -12.1877$, $P = 0.001$).

Among 170 1st-cycle specimens collected in October–June (37 Yellow-bellied, 25 Red-naped, 21 *ruber* Red-breasted, 59 *daggetti* Red-breasted, and 28 Williamson's sapsuckers, a subset of the 1st-cycle category in Table 1), completion of secondary-covert molt also appeared to be delayed in Yellow-bellied and Red-naped sapsuckers, but not as much as for the body feathers, appearing to complete by January in most individuals (Fig. 3). The other 3 taxa appeared to show little variation in completing most or all secondary-covert molt by the end of October, coinciding with completion of body-feather molt. Interestingly, all primaries and rectrices had been replaced on most or all birds by the end of October, apparently within the breeding range and prior to southbound migration.

Extent of the preformative molt

None of the 170 specimens collected in October–June had replaced any secondaries or primary coverts, and all of these had replaced all primaries and most or all upperwing lesser coverts (Supplemental Fig.
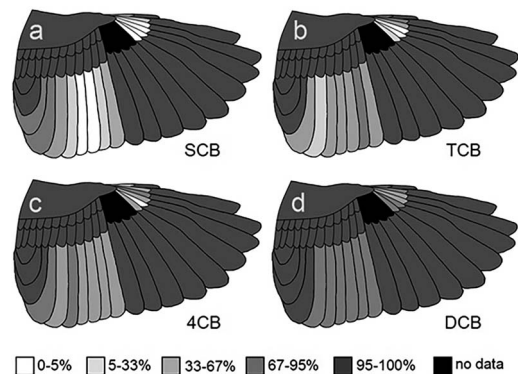
Figure 4. Replacement percentages for each alar feather among sapsuckers (all taxa pooled) in 2nd basic (SCB), 3rd basic TCB), 4th basic (4CB), and definitive basic (DCB) plumages. All individuals had replaced all secondary coverts and primaries. Percentages of primary coverts and secondaries replaced are based on feathers renewed during the most recent prebasic molt. Typical examples of replacement for each of these molts are shown in Supplemental Figure S3–S9 and percentages of feather replacement are shown in Table 2.

Table 2. Replacement percentages of each feather among pc5–pc10 and s1–s8 during prebasic molts in sapsuckers (all taxa pooled); pc1–pc4 could not be assessed in this study and s9–s10 appeared to be newly replaced in all birds. The 3 numbers in each cell indicate percentage of individuals in which each feather was juvenile, older basic, and newly replaced basic. In 4th basic plumage (but not definitive basic plumage), older basic feathers were further categorized as 1 or 2 years old (see text and Fig. 4).

Feather	2nd Prebasic	3rd Prebasic	4th Prebasic	Def. Prebasic
PC5	100/0/0	77/0/23	48/13/39	0/14/86
PC6	100/0/0	100/0/0	100/0/0	0/20/80
PC7	100/0/0	100/0/0	63/0/37	0/33/67
PC8	100/0/0	69/0/31	17/21/62	0/42/58
PC9	100/0/0	19/0/71	0/46/54	0/26/74
PC10	28/0/72	0/27/73	0/92/8	0/11/89
S1	34/0/76	0/52/48	0/63/37	0/20/80
S2	6/0/94	23/10/67	0/58/42	0/18/82
S3	0/0/100	46/0/54	0/58/42	0/21/79
S4	0/0/100	38/0/59	0/63/37	0/21/79
S5	15/0/75	13/37/50	0/67/33	0/20/80
S6	49/0/51	0/69/31	0/50/50	0/15/75
S7	17/0/83	0/38/62	0/21/79	0/3/97
S8	5/0/97	0/0/100	0/4/96	0/2/98

S2–S3). Replacement of larger secondary coverts ranged from the inner 3 median coverts only and no greater coverts replaced (Williamson's Sapsucker MVZ 102202) to all median coverts and the inner 8 greater coverts replaced (Yellow-bellied Sapsucker MVZ 73050). Overall linear models indicated no significant relationship between mean composite molt score and month, taxa or interactions thereof ($F_{9,149} = 1.285$, $P = 0.249$, Adj. $R^2 = 0.0160$), with the assumption of the normality of residuals met ($D = 0.0558$, $P = 0.706$).

Sequence and extent of prebasic molts and age determination

All 384 specimens of sapsuckers in 2nd and later basic plumages had replaced all upperwing secondary coverts, primaries, and rectrices, and most or all had replaced at least the inner 2 tertials, s10–s11 (Fig. 4, Supplemental Fig. S3–S9). All appeared to have also replaced all feathers by the end of October, prior to southbound migration. None of the 120 sapsuckers in 2nd basic plumage had replaced the 6 primary coverts pc3–pc8 and 2 secondaries s3–s4; the outermost primary covert (pc10) was replaced by only 33 of those birds (27.5%) and the 2nd covert (pc9) by

10 birds (12%) (Fig. 4a, Table 2). Individuals in 3rd basic plumage had retained 2–5 juvenile primary coverts (including at least pc6–pc7) and up to 4 juvenile secondaries among s1–s5 (Fig. 4b, Table 2). The juvenile outermost primary covert (p10) had been replaced in all birds and was newly basic in 77% of specimens and 1-year-old basic in 23% of specimens (Table 2). Juvenile secondaries were retained in 22 of 52 birds in 3rd basic plumage (42.3%), with the most birds retaining the juvenile s3, followed by s4, s2, and s5 (Fig. 4b, Table 2). Three birds had retained only the s3 and 1 had retained only the s4, indicating that either s3 or s4 could also be the terminal feather molted (Fig. 4b). That no individual showing this pattern of secondary replacement had retained only 1 juvenile primary covert indicates that all birds in 3rd basic plumage should be identifiable by retaining at least pc6 and pc7 and by having either juvenile or newly replaced (but not year-old basic) s3 and/or s4.

Some birds in 4th basic plumage were identified by the presence of at least 1 retained juvenile primary covert among pc5–pc8 and new and older basic primary coverts and secondaries showing patterns indicating at least 2 prior molts (Fig. 4c; Table 2). Despite differences in molt extents (see below), 3–6 individuals in 4th basic plumage were identified in all 5 taxa. The juvenile primary covert pc6 was retained in all individuals, followed by retention of pc7 in 63% of individuals, pc5 in 48% of individuals, and pc8 in 17% of individuals (Table 2). This indicates that pc6 is typically the terminal feather of replacement within the primary covert tract (Fig. 4c). It is highly probable that an unknown proportion of birds in 4th basic plumage had replaced all juvenile primary coverts and were indistinguishable from those categorized here as in definitive basic plumage. Likewise, it also seems probable that some birds in 5th basic plumage (5th/6th calendar years) had continued to retain 1 or more juvenile primary coverts and were categorized here as in 4th basic plumage.

Sapsuckers in definitive basic plumage showed uniformly replaced or mixed new and older basic primary coverts and secondaries, without juvenile feathers remaining (Fig. 4d, Table 2). All 6 visible primary coverts and all 10 secondaries appeared to be uniformly replaced during the previous prebasic molt in 72 of 189 individuals (38.1%), with at least 1 older basic primary covert being found
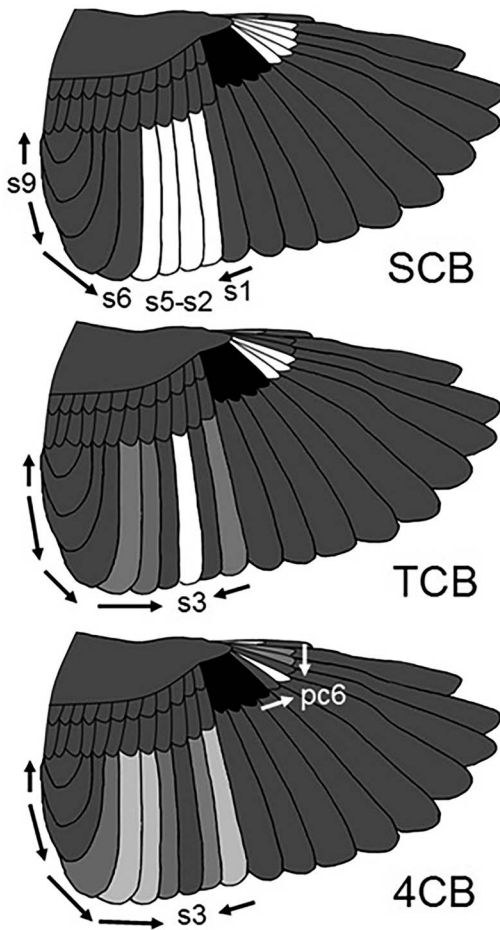
Figure 5. Progression of molt for a typical sapsucker from 2nd basic to 4th basic plumage. Juvenile feathers remaining are s2–s5 and pc5–pc9 in 2nd basic plumage (SCB), s3 and pc5–pc7 in 3rd basic plumage (TCB), and pc6 in 4th basic plumage (4CB). Juvenile feathers are white and gray shades among basic feathers represent molt clines, from older feathers (pale gray) to newer feathers (dark gray). Based on evidence from all prebasic molts, secondaries show a Staffelmauser-like pattern, the replacement sequences (bidirectionally from s9 and proximally from s1) being repeated with each ensuing molt, beginning where the previous molt was arrested and initiating new replacement waves in sequence from each node. Staffelmauser-like patterns appear also to occur among primary coverts, with repeated sequences from each end to the tract, terminating at pc6.

in 62.9% of birds and at least 1 older basic secondary being found in 41.3% of birds. In some definitive basic sapsuckers, 2 generations of older basic feathers appeared to be present (cf. Supplemental Fig. S3–S4) but distinguishing 1-year and 2-year or older retained feathers was considered too

imprecise to perform meaningful statistical analyses of basic feathers retained for more than 1 year. See Supplemental Figure S3–S9 for more details and the application of molt patterns to determine age through the 4th cycle (4CB or 4Y/5Y).

Evaluation of these replacement patterns and molt clines in specimens and images indicated that primary coverts are replaced centrifugally from each end of the tract, with a distal node from pc1, a proximal node from pc10, and with pc6 the last feather replaced as noted above (Fig. 5, Table 2, Supplemental Fig. S3–S9). Secondaries are also replaced centrifugally, with bilateral replacement node from the 2nd tertial (s9) in at least some cases and proximal replacement from the outermost secondary (s1), with s3 or s4 the last feathers replaced as noted above. Our results further indicate that sapsuckers undergo a Staffelmauser-like molting pattern within both tracts, with the feather replacement sequences being maintained, arrested following incomplete replacement, and both resumed in sequence and with new sequences initiating during subsequent prebasic molts (Fig. 5 and Supplemental Fig. S3–S4). These patterns are especially evident in images of birds recaptured at banding stations over multiple years (Supplemental Fig. S5–S9).

Extents of prebasic molts as related to age and taxon

An overall model showed a significant positive trend in mean composite molt score and molt cycle with older birds replacing more feathers annually (Fig. 6; $F_{9,373} = 88.69$, $P < 0.0001$, Adj. $R^2 = 0.673$).
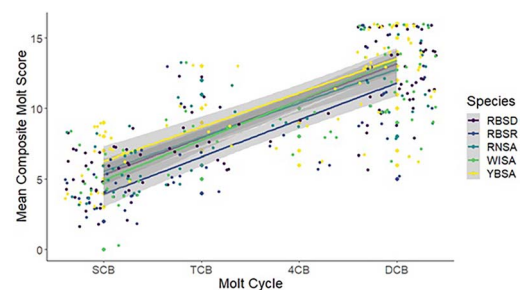
Figure 6. Mean number of primary coverts and secondaries replaced (composite molt score) during the prebasic molts preceding 2nd basic (SCB), 3rd basic (TCB), 4th basic (4CB), and definitive basic (DCB) plumages among 5 taxa of sapsuckers. See Figure 2 for species codes. Points are randomly jittered on the *x*-axis to help visualize sample size.

Although residuals did not meet the assumption of normality in distribution (KS-test: $D = 0.0799$, $P = 0.0150$), we believe that the robustness of these results indicates biologically meaningful relationship. All taxa showed a similar relationship between composite molt score and molt cycle (Fig. 6), and pairwise comparisons indicate there were no significant differences in these trends between taxa (Supplemental Table S3). On average, individuals in definitive prebasic plumage had a mean composite molt score that was 2.6 times higher than birds in their second basic plumage (13.2 ± 0.208 SE vs. 5.1 ± 0.167 SE). Among taxa, molt extent was significantly higher in Yellow-bellied Sapsucker than in other taxa except Williamson's Sapsucker, which in turn was significantly greater than those of Red-naped and *ruber* Red-breasted sapsuckers, and among Red-breasted Sapsuckers, molt was significantly greater in *daggetti* than in *ruber* (Supplemental Table S3).

Discussion

Extents of molts and age determination in sapsuckers

Our results support the concept that sapsuckers replace fewer feathers on average during preformative and prebasic molts than other North American woodpeckers. Pyle and Howell (1995) and Pyle (2022a) indicate that other North American woodpeckers can replace all upperwing secondary coverts and 1 or more tertials during the preformative molt, whereas no sapsuckers showed this pattern; at most all median coverts and 8 of 12 inner greater coverts were replaced and no tertials were replaced during the preformative molt. Following the 2nd prebasic molt (in SCBs or SY/TYs), most woodpeckers have replaced 1–5 outer primary coverts whereas in sapsuckers 72.5% of individuals had replaced no primary coverts, 27.5% had replaced the outer covert, and 12% of these had replaced the outermost 2 coverts. The number of juvenile primary coverts and secondaries retained during the 2nd and 3rd prebasic molts, furthermore, averages more than reported for other North American species (Pyle and Howell 1995, Siegel et al. 2016, Pyle 2022a).

Our results suggest that all sapsuckers in 3rd basic plumage (TCB or TY/4Y) can be identified by retaining at least 2 juvenile primary coverts (pc6–pc7). That none of these birds had retained just 1 covert suggests that none had also molted all coverts, although our methodology cannot exclude some birds undergoing a complete 3rd prebasic molt or having retained 1 covert and been designated as in 4th basic plumage. Our results further indicate that a proportion of sapsuckers in 4th basic plumage (4CB or 4Y/5Y) can be identified by the continued retention of at least 1 juvenile primary covert (pc6), a novel finding among woodpeckers and most other bird species with the exception of some owls and large flighted birds exhibiting Staffelmauser molting patterns (Pyle 2008, 2022a). It seems quite possible that some birds in 5th basic plumage (5CB or 5Y/6Y) may continue to retain juvenile primary coverts. The results of this paper expand our ability to age sapsuckers over the criteria presented in Pyle (2022a), in which definitive basic plumage referred to 3rd basic plumage or later and identification of 4th basic plumage is not indicated. Details on age determination in woodpeckers through the 3rd and 4th cycles are presented as Supplementary Materials (Fig. S2–S9, Table S4).

There were significant positive relationships between molt cycle and extent of feather replacement in all 5 taxa. Individuals in definitive basic plumage replaced over twice as many feathers annually as those in 2nd basic plumage. We propose that this is due to birds with more foraging experience being better at nutrition uptake and replacing more feathers on average. Only older birds (in at least 4th basic plumage) appeared to acquire the resources to undergo complete prebasic molts. In some large birds, the 2nd prebasic molt can average greater in extent than subsequent molts (Pyle 2008), but, unlike in sapsuckers (Gyug et al. 2020; Walters et al. 2020a, 2020b, 2020c), these species typically do not breed at 1 year of age and thus do not have breeding-related time constraints which may inhibit the 2nd prebasic molt (Pyle 2008).

Feather replacement sequences and strategies in sapsuckers

Hormonal and/or neurological processes leading to avian feather-replacement sequences and connectedness between feather tracts is little studied (Voitkevich 1966, Pyle 2013). Unlike locations, extents, and timing of molts, replacement sequences

within remiges appear to be evolutionarily fixed (Pyle 2013). In most birds, primaries and primary coverts are replaced sequentially, distally, and concurrently, from p1 to p10 and pc1 to pc10, and secondaries are replaced distally from the tertials and proximally from the outermost feather (s1). When exceptions to these sequences occur, they are usually found within all related species (Pyle 2008, 2013, 2022a).

In sapsuckers and other woodpeckers, replacement of primary coverts is convergent and unrelated to replacement of primaries. This sequence and its asynchrony with that of primaries is, thus far, known only in woodpeckers and certain kingfishers, those of subfamily Cerylinae at least (Pyle 2022a; CAS 100185 with pc6s on each wing retained, a distal molt cline from pc1 to pc5, and a proximal molt cline from pc10 to pc7). This unique primary-covert replacement sequence in woodpeckers and some kingfishers may indicate that it evolved prior to the split of Piciformes and Coraciiformes (cf. Pyle 2013); further study on closely related orders such as Trogoniformes, Bucerotiformes, and Galbuliformes could address this hypothesis. Another general example of asynchrony of primary and primary covert replacement is among "eccentric" preformative molt in some passerines, during which outer primaries but not always the corresponding primary coverts are replaced (Pyle 2022a). During eccentric preformative molts, however, sequence of primary covert replacement corresponds to that of the primaries in being distal (Pyle 1998, 2022a, 2022b; Jenni and Winkler 2020). The replacement sequence of secondaries, bilaterally from the 2nd tertial and proximally from the outermost feather, is common to other birds; however, the terminal feather, s3 or s4, is toward the distal rather than the proximal end of the tract, for example, typically at s5 or s6 among the 9 secondaries of passerines (Jenni and Winkler 2020, Pyle 2022a). Differences in sequence and terminal secondary may be related to adaptive features of wing shape and flight, as found among Falconiformes and Psittaciformes (Pyle 2013).

Our results indicate that both secondaries and primary coverts of sapsuckers are replaced in Staffelmauser-like (or stepwise-like) patterns (Stresemann and Stresemann 1966, Pyle 2006). This constitutes

the first report of Staffelmauser among primary coverts but not among primaries. Staffelmauser has been proposed as a strategy in birds that have insufficient time to complete prebasic molts but enabling replacement of as many feathers as possible without incurring large gaps in the wing that inhibit flight (Stresemann and Stresemann 1966, Tucker 1991, Shugart and Rohwer 1996, Pyle 2005). In sapsuckers and woodpeckers, primaries are typically replaced every year during both preformative and prebasic molts, indicating differing causal factors for Staffelmauser in woodpeckers. We propose that primary coverts and secondaries of sapsuckers and woodpeckers are replaced over multiple years to create a signal to others about age, experience, and/or quality of the individual for mate-selection purposes, as has been suggested for eccentric molt patterns in passerines (Pyle 1998).

An additional difference in the molting sequences of sapsuckers occurs with the relative timing of replacement between tracts during the preformative molt. Yellow-bellied Sapsucker, and to a lesser extent Red-naped Sapsucker, appear to retain and replace juvenile body feathers and secondary coverts well after molt of primaries, rectrices, and most upperwing secondary coverts has completed, an unusual between-tract molting strategy among birds. We propose that the retention of juvenile feathers well into winter and sometimes spring and summer is an adaptation for increased crypsis for 1st-year birds, which may afford extra protection from predation during migration and on the winter grounds. Prebasic molts of sapsuckers, on the other hand, appear to be completed rapidly on summer grounds, but basic body feathers are fringed buff, providing crypsis for these age groups as well.

Effects of migration strategy on the molts of sapsuckers

During the preformative molt, Yellow-bellied and to a lesser extent Red-naped sapsuckers delayed molt of body feathers relative to the other 3 sapsucker taxa, suspending it for migration in most cases. Extent of prebasic molts was also greater in Yellow-bellied and Williamson's sapsuckers and was lower in the *ruber* subspecies Red-breasted Sapsucker than the other taxa. With the exception of Williamson's Sapsucker, therefore, timing of the

preformative molt and extent of prebasic molts correlated positively with longer-distance migration. Our results on the preformative molt in sapsuckers is consistent with those of boreal breeding passerines, where migratory species are hypothesized to have more time available to complete molt on winter grounds rather than having it be constrained by the onset of winter (Hall and Tullberg 2004; Pyle 2008: p. 500–505; Kiat et al. 2019; Rueda-Hernández et al. 2023). We suggest that greater preformative molt extent in migratory sapsuckers is due largely to adaptation of molt strategies to the extent of solar exposure experienced on an annual basis, consistent with hypotheses based on migratory passerines (Pyle 1998, Terrill et al. 2020, Guallar et al. 2021, Kiat and Izhaki 2021, Rueda-Hernández et al. 2023). Yellow-bellied Sapsucker, and to a lesser extent Red-naped Sapsucker and the *daggetti* subspecies of Red-breasted Sapsucker, which also occupy relatively open habitats (Walters et al. 2020b, 2020c), experience more solar exposure on an annual basis than the more resident taxa. Williamson's Sapsucker breeds in sparser habitats than the other taxa and at higher elevations (Gyug et al. 2020), where it also may be exposed to more and higher intensity solar exposure. The *ruber* subspecies of Red-breasted Sapsucker, on the other hand, is largely resident and occurs in moister and more shaded habitats than the other taxa (Walters et al. 2020c). It thus follows that the increased degradation of feathers from solar exposure has resulted in taxa-wide adaptations to undergo more complete molts in breeding areas, preventing feathers that are retained for 2 or more years from becoming excessively abraded by solar exposure and compromising flight and foraging ability.

Modeling of age structure through the 3rd and, for a subset of individuals, the 4th basic plumages has the potential to inform conservation management decisions in sapsuckers, for example those related to salvage logging and habitat restoration (Siegel et al. 2016), as well as management to enhance habitats in which a greater proportion of older and more productive sapsuckers may be breeding (Pyle et al. 2020). Analysis of MAPS data indicates that survival is lower than expected in Yellow-bellied, Red-naped, and Red-breasted sapsuckers, with that of Yellow-bellied Sapsucker being especially low (DeSante et al. 2015). In general, highly migratory bird species appear to be suffering from lower survival than resident species, likely as related to increased mortality during migration, in turn due to habitat loss and increased weather severity with climate change (Sillett and Holmes 2002, DeSante et al. 2015, Paxton et al. 2017). Effects of climate change may also be detrimental to sapsuckers, especially for Williamson's Sapsucker, given its dependence on higher-elevation forest habitats and deeper snowpack, where climate change appears to be occurring more swiftly than at lower elevations (Siegel et al. 2014). Additional conservation and management concerns for sapsuckers include the effects of rapidly changing fire regimes, for which implications on woodpeckers and sapsuckers are not well understood (Saab et al. 2007, Gyug et al. 2020). We believe that the increased capacity of age determination that we document in this study (cf. Supplementary Materials) will help shed light on these conservation issues in sapsuckers.

Acknowledgments

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