CONCURRENT ECCENTRIC AND TYPICAL REPLACEMENT SEQUENCES DURING PREFORMATIVE MOLT IN THE SPOTTED TOWHEE

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ABSTRACT: Molt is a crucial component of the avian annual cycle, and precise knowledge of its extent, sequence, timing, and duration is key to understanding a species' life history. Differences in molt patterns allow individuals of most temperate-zone songbird species to be categorized as first-cycle or older. The extent of molt, however, can vary among individuals of a species, and knowledge of the frequency of unusually extensive or limited molts is critical for accurate age determination. During banding of 100 first-year Spotted Towhees (*Pipilo maculatus*) on Vancouver Island in autumn 2025, I noted two individuals in which the preformative molt was exceptionally extensive. In these individuals, up to six primaries, five secondaries, and seven primary coverts had been renewed. The patterns of these feathers' replacement had evidently followed eccentric and typical sequences concurrently, a combination previously documented in only seven North American passerine species. These results improve our understanding of molt in the Spotted Towhee and suggest that extensive replacement of juvenile flight feathers could improve the birds' fitness by furnishing higher-quality feathers that may enhance flight performance, thermoregulation, and resistance to wear, potentially providing an adaptive advantage in abrasive environments.

Accurately determining the age of birds is critical for numerous components of population-level analyses, such as breeding success and survival rates (Martin 1995). Age-related differences in plumage characteristics and molt patterns allow accurate discrimination of first-cycle birds from older individuals in most temperate-zone passerines. The majority of North American passerines undergo a partial preformative molt (renewing some but not all feathers) in their first year of life, and a complete prebasic molt (renewing all feathers) following the annual breeding season thereafter (Pyle 1997a, 2022a). Within a species, the extent of renewal of wing feathers during a preformative molt can vary considerably, both from individual to individual and from region to region (Mulvihill 1993, Pyle 1997a, Howell et al. 2003, Jenni and Winkler 2020a).

An eccentric molt is an incomplete molt that includes the renewal of outer primaries and inner secondaries to varying extents but not a block of consecutive inner primaries and outer secondaries. Sometimes the outer primary coverts are replaced, but usually most to all primary coverts are retained (Pyle 1997a, 2022a). During eccentric molts, the primary and secondary feathers are molted distally (Gargallo 2013, Pyle 2022b). In contrast, a typical preformative molt follows the sequence of the prebasic molt, in which primaries and primary coverts are molted distally, secondaries (among s1–s6) are molted proximally from the outermost, and tertials are molted bilaterally from the middle feather (Pyle 2022b). The only feathers that may be retained are among the outer primaries and primary coverts and the inner secondaries. As yet, concurrent eccentric and typical sequences during the preformative

molt have been documented in only seven species of North American passerines (Pyle 1997a, Small et al. 2013). When birds are aged by molt, precise knowledge of the species' strategy and extent of molt is essential to quantifying the prevalence of unexpected patterns.

Dwight (1900) recognized the presence or absence of a molt limit (a discontinuity between different generations of feathers) between the primary and greater secondary coverts as a reliable criterion for determining age in the Eastern Towhee (*Pipilo erythrophthalmus*). This limit results from a partial preformative molt that includes the greater secondary coverts but not the primary coverts. Sibley (1950) and Davis (1957) confirmed the same criterion in the other member of the Rufous-sided Towhee complex, the Spotted Towhee (*P. maculatus*). In first-year birds, the retained juvenile primary coverts are brownish and contrast with the renewed blackish (male) or slaty (female) greater secondary coverts. In adults, after the complete prebasic molt, these feathers are uniformly blackish or slaty across both tracts. Pyle (1997b) reported the preformative molt of these towhees to include all greater secondary coverts (except occasionally the outermost) and 1–3 tertials. Later, Johnson et al. (2013) showed that in a small proportion of Eastern Towhees the preformative molt could also be eccentric, as did Fettig and Hathcock (2015) for the Spotted Towhee, finding up to three outer primaries, three inner secondaries, and two outer primary coverts renewed.

Here, I present evidence of incomplete preformative molt consistent with having followed eccentric and typical replacement sequences concurrently in two Spotted Towhees on Vancouver Island in autumn 2025.

METHODS

Between 21 July and 18 October 2025, in accordance with the Canadian Migration Monitoring Network Protocol (Hussell and Ralph 2005), Spotted Towhees were captured during standardized banding at Rocky Point Bird Observatory's Rocky Point (48.321°, –123.547°) and Pedder Bay (48.350°, –123.578°) field stations in British Columbia, Canada. The banders mist-netted daily at both sites, with 13 nets at Rocky Point and 15 at Pedder Bay. Nets were opened 30 minutes prior to sunrise, operated for 6 hours, and checked and cleared every 20 minutes. All birds were captured under appropriate permits and in strict adherence with legal and ethical requirements.

The towhees' ages were determined by the presence or absence of molt limits in the wing coverts, with the extent of skull ossification used as a supplementary criterion when time allowed (McKinney 2004, Fettig and Hathcock 2015, Pyle 2022a). The birds were sexed by plumage color (Sibley 2014, Pyle 2022a). In the sample, I included only first-year birds in formative plumage. To document patterns of extensive feather replacement, I photographed the wings of the individuals in which any primary coverts had been renewed. Visible primaries and primary coverts are numbered distally (p1–p9 and pc1–pc8), and secondaries are numbered proximally (s1–s6). All individuals were of the subspecies *oreganus* on the basis of the extent of white on the scapulars, wing coverts, and rectrices (Pyle 2022a).

RESULTS

Two of 100 first-year Spotted Towhees captured from 4 September to 10 October had undergone a preformative molt more extensive than documented in prior literature (Pyle 1997a, Fettig and Hathcock 2015). A first-year female banded at Rocky Point on 23 September 2025 had replaced feathers in patterns that I inferred to have followed both eccentric and typical sequences. On the right wing, p1–p5 were retained and p6–p9 renewed; s1 and s2 were renewed, s3 retained, and s4–s6 renewed; pc1–pc3 were renewed, pc4 retained, and pc5–pc8 renewed (Figure 1). On the left wing, replacement of the primaries was symmetrical, but s1 and s2 were retained, s3 renewed, s4 retained, and s5 and s6 renewed; pc1–pc3 were renewed, pc4–pc5 retained, pc6 renewed, and pc7–pc8 retained (Figure 2). Similarly, a first-year male banded at Pedder Bay on 9 October 2025 had molted in patterns consistent with both eccentric and typical sequences. On the right wing, p1–p4 were retained and p5–p9 renewed; s1 was renewed, s2 retained, and s3–s6 renewed; pc1–pc4 were retained and pc5–pc8 renewed. On the left wing, p1–p3 were retained and p4–p9 renewed; s1 was renewed, s2 and s3 retained, and s4–s6 renewed; pc1 was renewed, pc2 retained, and pc3–pc8 renewed.

DISCUSSION

This study documents the most extensive instances of preformative molt yet recorded in the Spotted Towhee, with up to six primaries, five secondar-



FIGURE 1. Right wing of Spotted Towhee 3051-00417, a first-year female in formative plumage, banded at Rocky Point, British Columbia, on 23 September 2025, exhibiting a mix of renewed and retained feathers. The patterns of replacement are consistent with both eccentric and typical sequences. Primaries and secondaries (among p1–9 and s1–6) are labelled, with renewed remiges denoted by asterisks; those lacking an asterisk are retained juvenile feathers.

Photo by Max Hellicar



FIGURE 2. Primary coverts on the left wing of Spotted Towhee 3051-00417, a first-year female in formative plumage, exhibiting a mix of renewed (denoted by asterisks) and retained feathers, banded at Rocky Point, British Columbia, on 23 September 2025.

Photo by Max Hellicar

ies, and seven primary coverts renewed, expanding the upper bounds of the extent of preformative molt in each of these feather tracts and increasing the sample size of molt examined in the species (Pyle 1997a, Fettig and Hathcock 2015). Notably, I provide the first documentation of concurrent eccentric and typical replacement sequences during the preformative molt in the species. These patterns occurred in two individuals, representing 2% of the first-year Spotted Towhees examined on Vancouver Island in autumn 2025. In both individuals, although replacement of outer primaries, inner secondaries and outer primary coverts followed an eccentric sequence, replacement of the outer secondaries and inner primary coverts was consistent with the typical sequence (Figure 1).

With any unexpected pattern of replacement, the possibility of a feather's accidental loss and adventitious replacement (Humphrey and Parkes 1959) should be considered. In the cases of the two towhees I describe, multiple factors signify that these molt patterns arose intrinsically (Jenni and Winkler 2020b). Simultaneous loss of numerous remiges reduces a bird's flight capability and therefore probability of survival. Additionally, the similarity in replacement patterns between the left and right wings of each towhee is unlikely to have arisen by accident. Furthermore, the patterns of feather replacement in these Spotted Towhees are similar to those in other species in which concurrent eccentric and typical sequences have been identified.

In New Mexico, Fettig and Hathcock (2015) reported an eccentric preformative molt in one first-year male Spotted Towhee among a sample of 30 individuals in formative plumage. It had renewed p7–p9 (right wing) and p7–p8 (left wing), s4–s6 on both wings, pc8–9 (right wing) and pc7 (left wing), representing the first documented eccentric molt in the species. Also within the Rufous-sided Towhee complex, Johnson et al. (2013) recorded three of

27 formative-plumaged Eastern Towhees to have undergone an eccentric preformative molt, including a variable extent of outer primaries and inner secondaries but no primary coverts. Tattoni et al. (2022) detailed the renewal of remiges during eccentric preformative molt in five California (*Melozone crissalis*) and two Canyon Towhees (*M. fusca*). None of these, however, had renewed any primary coverts. During their first year of life, most temperate-zone passerines do not molt their primary coverts (Pyle 1997a, Jenni and Winkler 2020a), which are the feather tract least commonly renewed during the preformative molt (Kiat and Izhaki 2017). Those that do molt primary coverts, however, tend to replace them only when primaries are also being renewed, but may not molt the primary covert that corresponds with each renewed primary (Westphal et al. 1976, Gargallo and Clarabuch 1995), a pattern consistent with my findings (Figure 2).

Among 54 species of North American passerines that can undergo incomplete preformative molt, Pyle (1997a) found eccentric sequences in 46, typical sequences in eight, and both concurrently in six. Of these six species, the Blue Grosbeak (*Passerina caerulea*), Lazuli Bunting (*P. amoena*), Varied Bunting (*P. versicolor*), Carolina Wren (*Thryothorus ludovicianus*), House Finch (*Haemorhous mexicanus*), and Song Sparrow (*Melospiza melodia*), only 5–16% of individuals that had molted in an eccentric sequence had also replaced some feathers in the typical sequence (Pyle 1997a). Later, Small et al. (2013) found concurrent eccentric and typical sequences of replacement during preformative molt in 8% of the Field Sparrows (*Spizella pusilla*) they examined. The Spotted Towhee becomes the eighth North American passerine species, and the third in the family Passerellidae, in which both replacement sequences are documented.

Even within a species, passerines' preformative molt may range from partial to complete (Pérez and Brandolin 2024). Subspecies or populations may differ in the extent of this molt, as in the Song Sparrow (Hudson et al. 2008). Johnson et al. (2013) predicted, on the basis of their findings in the Eastern Towhee, that further examination of the Spotted Towhee would reveal eccentric preformative molt in a small percentage of birds, which my findings, along with those of Fettig and Hathcock (2015), support. Although a complete preformative molt has never been recorded in the Rufous-sided Towhee complex, the extent of replacement documented suggests the possibility warrants consideration. Although the presence or absence of molt limits is considered a reliable method to age Rufous-sided Towhees (Johnson et al. 2013, Fettig and Hathcock 2015), I encourage banders to check flight feathers for evidence of extensive preformative molt, and the extent of skull ossification (McKinney 2004, Pyle 2022a) may be useful for confirming the age of apparent adults in autumn. Despite iris color having long been regarded as a basis for assessing age in the Spotted Towhee (Davis 1957), Hohn et al. (2025) found extensive overlap in iris color among demographic groups, lessening its reliability as a criterion for age. Therefore, molt limits, and the patterns and extent of molt from which they arise, are important considerations in assessment of a Spotted Towhee's age.

When birds undergo preformative molt, they attain higher-quality plumage, which may improve their fitness (Kiat and Izhaki 2016, Podlaszczuk et al. 2016). Juvenile feathers grown in the nest are simpler in structure, having

fewer barbs per unit length, and are typically weaker than the feather generations succeeding them (Kiat and Izhaki 2016, Podlaszczuk et al. 2016). This is because nestlings prioritize fast growth of the juvenile plumage at the expense of feather quality (Butler et al. 2008). Therefore, in species that retain juvenile plumage beyond the preformative molt, those feathers' lower quality may impair fitness (Podlaszczuk et al. 2016). Feathers with greater structural quality improve flight performance and thermoregulation (Nilsson and Svensson 1996, Swaddle et al. 1996) and better resist wear and abrasion (Dawson et al. 2000). The adaptive value of an extensive preformative molt may be particularly pronounced in species exposed to conditions that accelerate feather wear and weaken feathers' structural integrity, such as abrasive vegetation and intense solar radiation (Willoughby 1991, Pyle 1998, Jenni and Winkler 2020a). The renewal of flight feathers in first-year Spotted Towhees, which inhabit thickets that are often abrasive (Bent 1968), may improve the birds' fitness by reducing the proportion of weaker feathers that have been exposed to substantial wear and increasing the proportion of fresher, higher-quality feathers.

Molt is an energetically and nutritionally costly process (Murphy and King 1992). There is a limit to the number of feathers first-year birds can replace without significantly compromising other needs (Delhey et al. 2020). Alternatively, variation in the preformative molt's extent may be neutral, arising and persisting in the absence of strong selective pressures. Wolfe et al. (2021) suggested that the pervasiveness of preformative molt in passerines is not currently adaptive, representing a vestigial trait, potentially leaving its extent somewhat unconstrained by contemporary selection. Variation in the extent of molt may also arise from constraints associated with time and resource availability (Delhey et al. 2020).

The southern subspecies of the Spotted Towhee average slightly greater in extent of preformative molt than those in the north (Pyle 1997b). Therefore, the incidence of extensive preformative molt at the northern edge of the species' range (Sibley 2014) is noteworthy, paralleling reports in Song Sparrow (Hudson et al. 2008). With the Spotted Towhee consisting of 21 recognized subspecies (AviList Core Team 2026), of which only one is represented in this study, further research, particularly farther south, may reveal extensive preformative molt to be more frequent in the species than previously reported.

Documentation of unusual molt patterns improves understanding of their prevalence, and improved knowledge on the variation in species-specific molt patterns enhances the accuracy of age determination. In turn, accurate age determination improves avian population monitoring and conservation.

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