NOTES

INCIDENCE AND EXTENT OF ECCENTRIC PREFORMATIVE MOLT IN THE CALIFORNIA AND CANYON TOWHEES

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Temperate-zone passerines undergo a preformative molt during their first cycle, typically within a few weeks or months after fledging (Howell et al. 2003). For most species, this molt is partial, encompassing all body and head feathers plus a variable number of wing coverts but no remiges or rectrices (Pyle 1997a). In some species, however, the preformative molt also includes a variable number of flight feathers. One common pattern of such incomplete molt is an eccentric replacement in which the outermost primaries and the innermost secondaries are replaced (Pyle 1997a, 1998). These patterns are useful among researchers who capture and band wild birds as they distinguish individuals in their first plumage cycle from those in their definitive cycle, in which all remiges are replaced (Pyle 1997a).

Previous publications on the preformative molt of the California Towhee (*Melozone crissalis*) describe it as including all the head and body feathers, most to all the lesser, median, and greater coverts, and sometimes 1–3 tertials and 2–12 rectrices (Pyle 1997a, Benedict et al. 2011). The preformative molt of the Canyon Towhee (*M. fusca*) follows the same pattern but the occasional replacement of flight feathers is less extensive, extending to only 1–2 tertials and 1–4 rectrices (Pyle 1997a). We found no published evidence that first-cycle towhees of either species replace outer primaries during this molt. Furthermore, we reviewed the literature on the molt patterns of the other six species in the genus *Melozone* and found no specific documentation of eccentric replacement of remiges in the preformative molt. The possibility is implied, however, by Pyle's (1997a) mention in his account of Abert's Towhee (*M. aberti*) that "reports that the [preformative] molt can include [rectrices] and [primaries] require verification," and Tweit and Finch's (1994) reference to unpublished data that 11% of hatch-year birds captured at a banding station in Arizona had replaced primaries. Nevertheless, molt has been little studied in this genus, so the lack of published evidence should not be interpreted as a lack of eccentric molt. Towhees of the genus *Pipilo* have been documented replacing outer primaries in an eccentric pattern during the preformative molt (Johnson et al. 2013, Fettig and Hathcock 2015), and this pattern is documented in several other North American sparrow species (Pyle 1997a).

Here we present evidence for incomplete preformative molt of remiges following an eccentric pattern among five California Towhees banded in the San Francisco Bay region, California, and two Canyon Towhees banded near Los Alamos, New Mexico. Our data come from four landbird-banding stations: (1) the Coyote Creek Field Station in Milpitas, California (operated 1987–2021), (2) an unnamed temporary station ~5 km upstream of there (operated 2002–03 and 2007–08), the Los Trancos Creek Banding Station in Portola Valley, California (operated 2019–2021), and a station operated by the Los Alamos National Laboratory in Los Alamos County, New Mexico (operated 2010–2021).

FIGURE 1. Right wing of a first-cycle Canyon Towhee (*Melozone fusca*) captured near Los Alamos, New Mexico, on 18 October 2018 showing evidence of an incomplete preformative molt following an eccentric pattern. P9 and S6–S9 have darker bases and shafts and are less worn than the other flight feathers. Importantly, the primary coverts appear uniform and retained from the earlier generation of juvenile feathers. An asterisk (*) indicates feathers that represent the formative plumage.

Photo by Charles D. Hathcock

Banding at and near the Coyote Creek Field Station was conducted by staff and volunteers of the San Francisco Bay Bird Observatory. The Coyote Creek Field Station operates in a standardized way on Wednesdays, Saturdays, and Sundays every week of the year, conditions permitting. Non-overlapping arrays of 14, 14, and 19 mist nets are operated on each of these days, respectively. During the years the station 5 km to the southeast was active, 18 nets were operated approximately once per week. A project of researchers at Stanford University, the Los Trancos Creek station was operated approximately once per week and comprised 7 nets. Banding at Los Alamos was conducted by researchers at the Los Alamos National Laboratory. That station was operated once per week during fall migration from mid-August through mid-October and had 14 mist nets.

At each station, mist nets were opened approximately 30 minutes prior to local sunrise and closed 5 hours after opening. Nets were checked at a minimum of once every 30 minutes and trained personnel extracted all birds. Each new bird was given an appropriately sized USGS metal leg band and standard data were recorded. Recaptures were processed similarly. See Barton and Sandercock (2017) for a more detailed description of the stations' operation. We number primaries from innermost (P1) to outermost (P9) and secondaries from outermost (S1) to innermost (S9; the tertials being S7–S9) as is standard in studies of molt.

On 18 October 2018, we captured a first-cycle Canyon Towhee with an eccentric pattern of flight-feather replacement at Los Alamos (Figure 1). We noted that P9

FIGURE 2. Right and left wings of a first-cycle California Towhee (*Melozone crissalis*) captured at the Los Trancos Creek Banding Station, California, on 23 October 2021 showing evidence of an incomplete preformative molt following an eccentric pattern. P8–P9 and S7–S9 have darker bases and shafts and are less worn than the other flight feathers. Importantly, the primary coverts appear uniform and retained from the juvenile plumage. An asterisk (*) indicates feathers that represent the formative plumage.

Photo by D. Julian Tattoni

and S6–S9 had darker bases, darker shafts, and less wear than the other flight feathers, suggesting they were replaced in a more recent molt. The primary coverts were uniformly dull brown, matching the apparently older flight feathers, which ruled out the possibility of a suspended pre-basic molt (P. Pyle pers. comm.). On 23 October 2021, we encountered a first-cycle California Towhee with a similar eccentric pattern of flight-feather replacement at Los Trancos Creek (Figure 2). Again, we noted that P8–P9 and S7–S9 had darker bases, darker shafts, and less wear than the other flight feathers and that the primary coverts were dull brown, matching the flight feathers retained from the earlier plumage. Furthermore, when this individual was originally banded on 8 August 2021, its skull was incompletely ossified, additional support for its being a first-year bird that had undergone an incomplete preformative molt following an eccentric pattern rather than an adult that had suspended its pre-basic molt (P. Pyle pers. comm.).

These unusual captures prompted us to review all records of California and Canyon Towhees banded under our organizations' federal banding permits (22109 and 23440), and we found five other instances (six total) of incomplete preformative molts following an eccentric pattern in these species. Across our three banding sites in California, records for 5/369 (1.4%) individual first-cycle California Towhees had documentation of eccentric molt (Table 1). The detection of eccentric molt patterns varied dramatically between our three study sites, representing 2/358 (0.6%) of the towhees captured at the Coyote Creek Field Station, 1/6 (16.7%) of those captured 5 km upstream of the Coyote Creek Field Station, and 2/5 (40%) of those captured at Los Trancos Creek. At our station in New Mexico, we documented eccentric molt in 2/21 (9.5%) first-cycle Canyon Towhees captured (Table 1).

Among the five California Towhees with eccentric replacement, all had replaced P9, 4/5 had also replaced P8, 2/5 had also replaced P7, and 1/5 had also replaced

Table 1 Wing-Molt Data for First-Cycle California and Canyon Towhees Captured with an Eccentric Pattern of Incomplete Preformative Molt[a]

		Primaries									Secondaries								
Species and site	Date	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9
California Towhee																			
5 km SE Coyote Cr. Field Sta.																			
	14 Nov 2002	F	F	J	J	J	J	J	J	J	U	U	U	U	U	U	U	U	U
Coyote Cr. Field Sta.																			
	5 Oct 2003	F	F	F	F	F	J	J	J	J	J	J	J	J	J	J	U	U	U
	4 Aug 2007	G	G	G	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J
Los Trancos Cr.																			
	16 Oct 2019	F	J	J	J	J	J	J	J	J	J	J	J	J	J	G	J	G	J
	23 Oct 2021	F	F	J	J	J	J	J	J	J	J	J	J	J	J	J	F	F	F
Canyon Towhee																			
Los Alamos National Laboratory																			
	10 Oct 2018	G	G	J	J	J	J	J	J	J	J	J	J	J	G	G	J	J	J
	18 Oct 2018	F	J	J	J	J	J	J	J	J	J	J	J	J	J	G	G	G	G

[a]J, juvenile; F, formative; G, growing (formative); U, unknown.

P6 and P5 (Table 1). Data on the secondaries had been recorded for only four of these birds. Of these, two had replaced all three tertials (S7–S9) and one (25%) had replaced an additional inner secondary (S6) (Table 1). Of the two Canyon Towhees with eccentric replacement, both had replaced P9, while one had also replaced P8. With respect to the secondaries, one bird had replaced S5, both had replaced S6, and one had replaced all three tertials (S7–S9). The primary coverts of both Canyon Towhees were retained from the earlier plumage. In each case the molt was noted as symmetric, suggesting the outer primaries had been replaced during the preformative molt, not adventitiously.

The differences in detection of eccentric preformative molt among California Towhees at our California study sites were interesting considering all three sites are within 16 km of one another and in the same habitat. But sample sizes differed widely with greater and more consistent banding effort at the Coyote Creek Field Station than at the other sites, where the greater percentage of first-cycle California Towhees with eccentric molt patterns may be an artifact of the difference in sampling. Our satellite stations, however, are often operated by our most experienced banders, who may be more likely to notice and record atypical molt patterns. If this were the case, eccentric molt among first-cycle California Towhees may be under-detected at the Coyote Creek Field Station.

Many researchers and bird banders have proposed that incomplete preformative molt of remiges is adaptive for species living in dry, scrubby, and sun-exposed habitats where the juvenile feathers may be more exposed and so wear down rapidly (Pyle 1998, Pyle et al. 2004, Guallar et al. 2021), though little empirical evidence has been published. Guallar et al. (2021) have provided the strongest evidence for this hypothesis, demonstrating that within the Cardinalidae, the evolution of incomplete preformative molt following an eccentric pattern is correlated with transitions toward more open habitats.

Do our observations represent the appearance of adaptive traits within these populations, or are they merely aberrant molt patterns? Across their ranges, both the California and Canyon Towhees are ubiquitous in habitats that have many of the characteristics considered to be ecological drivers of the evolution of eccentric molt,

as they occupy open, sunny habitats with scrubby vegetation in dry climates (Johnson and Haight 1996, Benedict et al. 2011). The lack of evidence from specimens collected in the 19th and 20th centuries (Pyle 1997b) suggests eccentric molts did not provide substantial adaptive value for these species. However, the contemporary documentation at our study sites may indicate that these molt patterns are increasing in frequency and that under changing climatic and environmental conditions they may be beneficial. Interestingly, there is some initial evidence among western Palearctic species that the extent of preformative molt is increasing with rising global temperatures (Kiat et al. 2019). If eccentric molt is becoming adaptive at our study sites, we should expect to document more individuals with these patterns in the coming years.

Overall, our observations highlight a core question in the study of the avian molt: how do contemporary environments interact with evolutionary histories to produce the molt patterns we observe in extant birds? It is difficult to ascertain how much of a bird's current environment has shaped its molt pattern, especially considering how conserved patterns of molt appear to be across extant passerines (with all species following one of two main strategies, the "complex basic" or "complex alternate"; see Howell et al. 2003).

Our observations, together with those of other researchers documenting molt patterns considered atypical for a species (e.g., Hudson et al. 2006, Fettig and Hathcock 2015), suggest that within some populations there may be considerable individual variation in molt patterns. While the adaptive value of specific patterns remains poorly understood, when variation exists we may expect to see continuing evolution of molt patterns in response to environmental change.

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