The Plumages of the Pileated Woodpecker

The plumages of Pileated Woodpeckers, unlike those of Scarlet Tanagers and Laughing Gulls and Myrtle Warblers, don't seem to change all that much in time and space. At least not on first inspection. There is a reasonably well-known difference between male and female, although it involves a very small fraction of the surface area of the bird. All things considered, however, on the spectrum from Wrentits (no appreciable age/sex/season-related molt differences at all) to Bobolinks and Dark-eyed Juncos and Australian King-Parrots (huge variation in plumages seasonally, geographically, and sexually), Pileateds are arguably closer to the former. But look closer! Which is exactly what we're going to do in this photo-based appreciation of the 2021 ABA Bird of the Year, *Dryocopus pileatus*.

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Certain aspects of molt are variable: when in the year it happens, where geographically it occurs, and how much of the bird is affected. In contrast, the replacement sequences of a bird's primaries, secondaries, and primary coverts, both within and among these tracts, are relatively fixed in birds. Most bird species replace primaries from the innermost (p1) to the outermost (p9, p10, or p11) feather, while replacing primary coverts at the same time as their corresponding primaries. Among the secondaries, the tertials are usually replaced, beginning with the middle one, when p1 and p2 are molting. Subsequently, the outermost secondary, s1, usually drops about when p6 is molted, followed by proximal replacement toward the tertials.

These sequences are widespread and consistent, indicating that they are ancestral in birds. Indeed, it has recently been shown that the paravian dinosaur *Microraptor*, a precursor to birds, replaced its feather-like scales in a similar sequence, a discovery reported in 2020 by Yosef Kiat and collaborators in *Current Biology* (tinyurl.com/dinosaur-molt). When an ancestral bird lineage deviates from this pattern, as have falcons and parrots for example, the altered sequence is often found throughout all taxa along the line; see my 2013 paper in *The Condor* (tinyurl.com/Pyle-parrots-falcons).

Sometime during the ancestral evolution of woodpeckers, molt replacement patterns took a radical turn. Woodpeckers are the only family of birds that typically replace all of their juvenile primaries and rectrices during an incomplete preformative (first-cycle) molt. Replacement of primary coverts, furthermore, does not at all track this primary replacement, which begins even before a young woodpecker leaves the nest hole! It is thought that the inner one or two juvenile primaries are inherently short, but I think instead they get replaced with formative primaries while still growing themselves. In any event, all primary coverts and most or all secondaries are retained during the preformative molt in woodpeckers, a unique strategy for any bird molt that involves replacement of all primaries.

Even replacement of the rectrices is anomalous, with the central pair coming in last—as opposed to molting first in most birds. This adaptation is believed to be related to keeping these feathers as strong as possible for scaling trees. In most birds, prebasic molts are complete or nearly so,

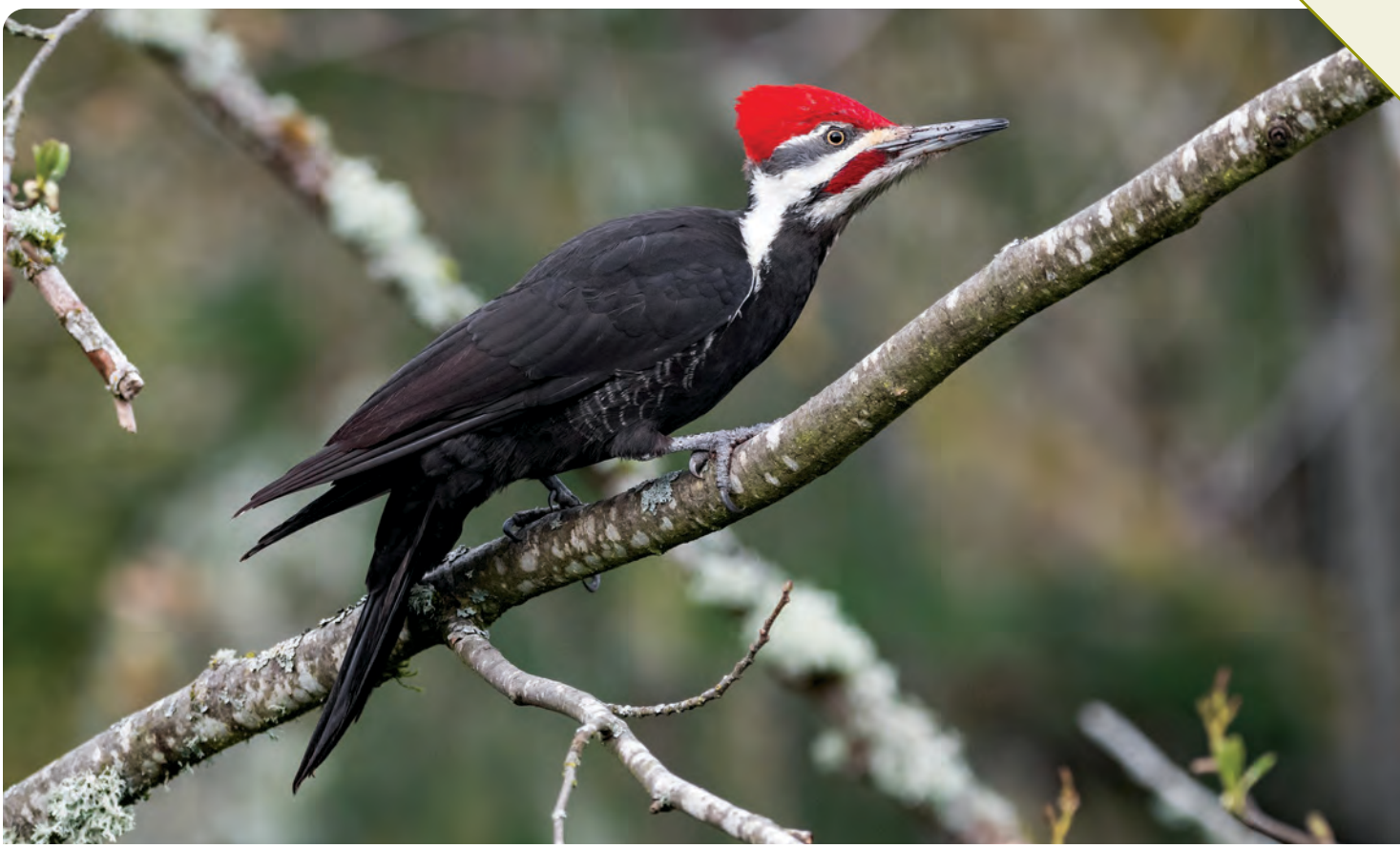


Fig. 1 • *King County, Washington; Apr. 3, 2020. Photo by © Mason Maron.* [macaulaylibrary.org/asset/220754371]

Woodpeckers begin the prefomative molt before leaving the nest and complete it within 1–2 months of fledging, usually by October in the ABA Area. In the Pileated Woodpecker, this molt typically includes all body feathers, primaries, and rectrices, some but not all proximal upperwing secondary coverts, and sometimes 1–3 tertials, but no primary coverts. By April, when this bird was photographed, the unmolted, juvenile secondary coverts, secondaries, and primary coverts are worn and brown, contrasting with the newer and darker, replaced, formative, back feathers and tertials. The primary coverts, the best tract for aging, are rarely visible in most images of woodpeckers, with the exception of those caught launching from a branch or trunk.

Here we can see the edges of 2–3 outer primary coverts, visible to the left of the alula, on the edge of the wing, above the white-tipped feathers of the sides. They appear uniform in wear and slightly browner than the replaced formative primaries, consistent with Fig. 5b in the 1995 paper by Steve Howell and me in the *Journal of Field Ornithology*. Turning to the other flight feathers, the tertials have been replaced and clearly contrast with the more worn juvenile outer secondaries, again matching our 1995 findings.

Finally, it looks like the greater coverts and at least some of the median coverts may be browner than some of the lesser coverts and the scapulars, representing a "molt limit" between juvenile and formative feathers, respectively. The evidence in these three tracts thus supports the determination that this is a bird in formative plumage, 10–11 months of age. But without being able to analyze the wing coverts more closely (for example, had the bird been in hand), there is some chance that this bird could be a year older; in this scenario, it would have replaced no outer primary coverts and retained most of the secondaries during the second prebasic molt. One such bird is depicted in Fig. 2; see also Fig. 5 for a formative bird that more clearly shows contrasts among secondary coverts.

but in woodpeckers both primary coverts and secondaries are often not replaced each year. Juvenile secondaries can be retained for two years. Juvenile primary coverts are always retained for two years and can be retained for three years! The identification of juvenile primary coverts and secondaries thus allows us to determine the age of some woodpeckers in their first three years of life.

I like puzzles and brainteasers, a prerequisite amusement to the study of bird molt. Before the mid-1990s, the anomalous molt patterns of woodpeckers were largely unknown. Ornithologists had recognized that woodpecker primaries are replaced during the preformative molt, beginning before fledging. But they wrote off the rest of it—if they noticed it at all—as either random variation or too hard to figure out. It took Steve Howell and me

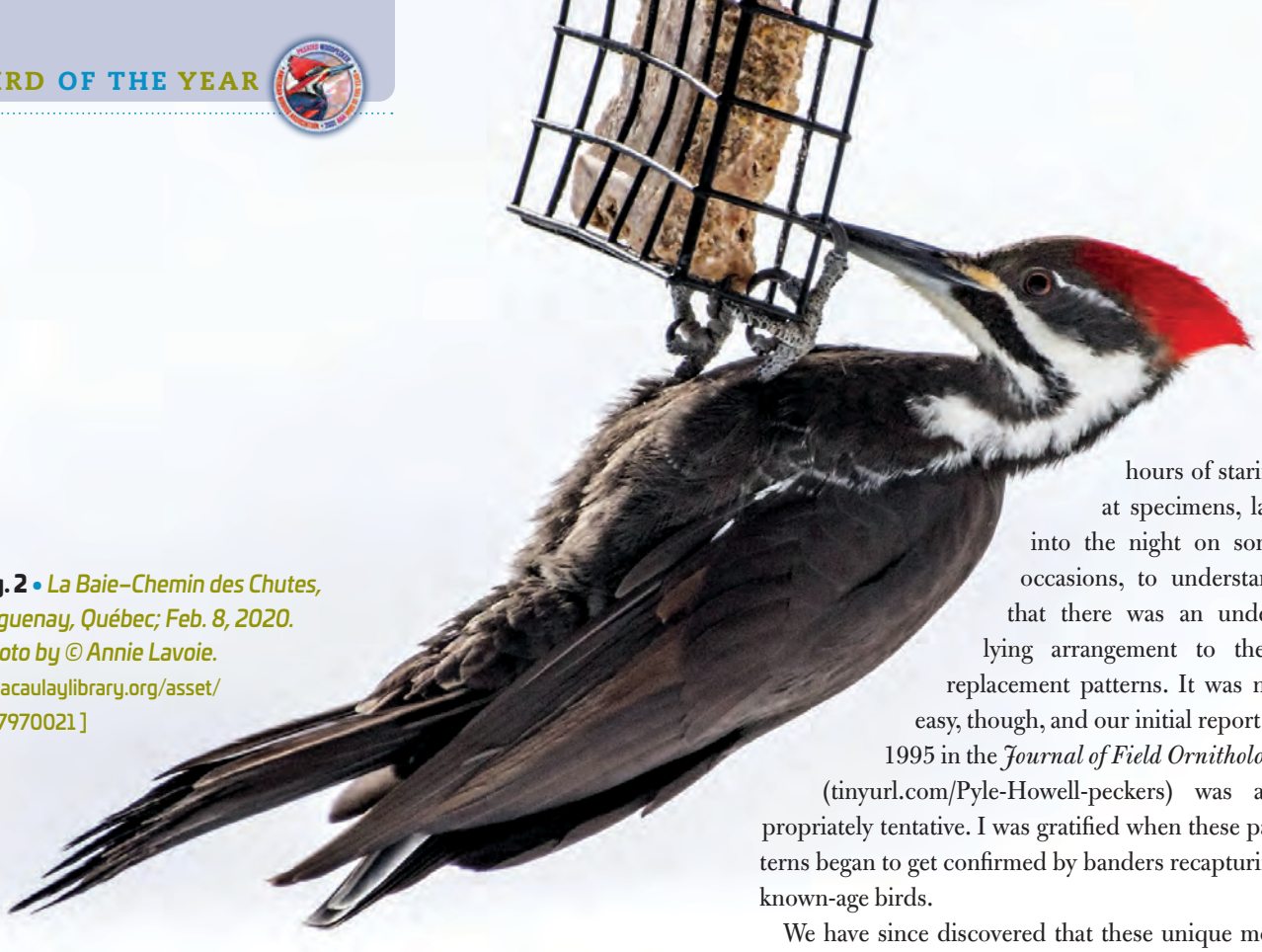


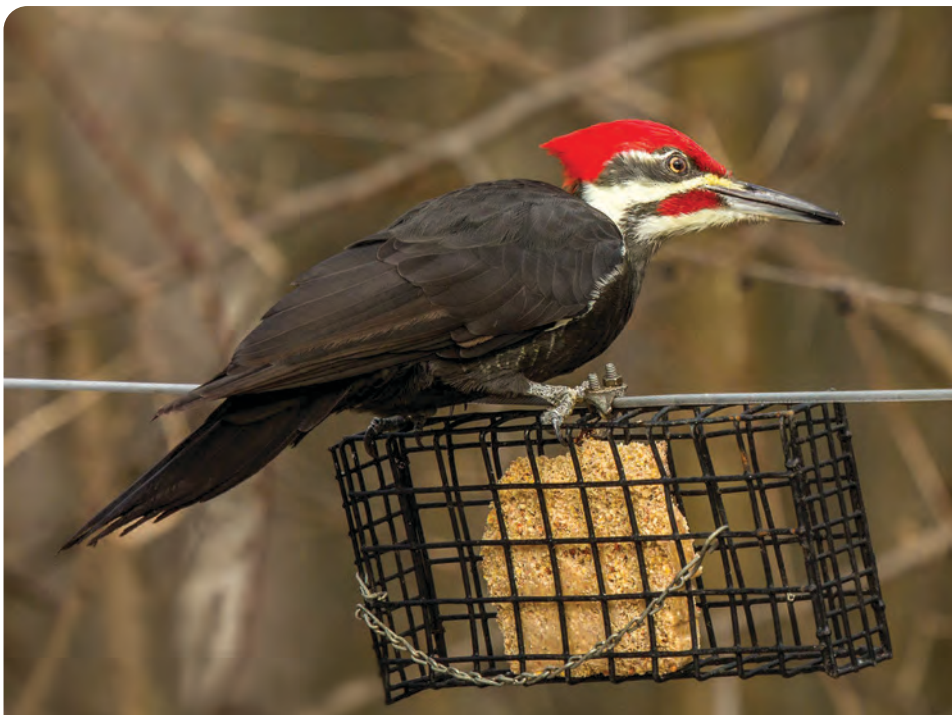
Fig. 2 • *La Baie–Chemin des Chutes, Saguenay, Québec; Feb. 8, 2020. Photo by © Annie Lavoie.* [macaulaylibrary.org/asset/207970021]

The second prebasic molt is where woodpeckers really begin to diverge from the molt strategies of most other birds. Unlike passerines, shorebirds, gulls, and many other species, woodpeckers sport juvenile primary coverts and secondaries that may be retained through this molt, thus remaining on the bird for at least two years. Recall that the pattern of replacement among these tracts in woodpeckers is fixed and predictable, such that when juvenile feathers are retained, we know where to look for and identify them. During the second prebasic molt, 0–5 outer primary coverts are replaced, usually leaving 4–8 juvenile coverts in the center of the tract, those corresponding to somewhere among p3–p10; the inner 1–2 primary coverts can also be replaced during this molt. This pattern seems to hold throughout the family Picidae, and is critical to age determination in woodpeckers.

In this Pileated Woodpecker, it looks like the outer three primary coverts have been replaced; the outermost is short and not visible. Working inward, the next three or more are retained juvenile feathers, being quite a bit browner than the replaced coverts; it is February, so these juvenile feathers are now 21–22 months old. Some Pileated Woodpeckers replace all secondaries during the second prebasic molt, while others can retain 1–5 juvenile secondaries among s2–s6. I think I can account for all 11 secondaries in this image, and I judge four secondaries, s3–s6, to be juvenile, matching in color and abrasion the retained juvenile primary coverts. Note how much more worn these juvenile feathers are than in the presumptive formative bird in Figs. 1 & 5. Finally, note that the secondary coverts appear to be of a single generation, all second basic, without the molt limits seen in formative birds. These patterns are classic for second-basic woodpeckers, as shown in Fig. 5c of my 1995 *Journal of Field Ornithology* paper with Steve Howell. See also Fig. 6, depicting a bird with a similar replacement pattern and extent.

hours of staring at specimens, late into the night on some occasions, to understand that there was an underlying arrangement to these replacement patterns. It was not easy, though, and our initial report in 1995 in the *Journal of Field Ornithology* (tinyurl.com/Pyle-Howell-peckers) was appropriately tentative. I was gratified when these patterns began to get confirmed by banders recapturing known-age birds.

We have since discovered that these unique molt sequences are rather fixed in the family Picidae, occurring in taxonomic outliers like piculets and wrynecks, in extinct species like Ivory-billed and Imperial woodpeckers (I have examined the specimens!), and in everything in between—including Pileated Woodpeckers. Preliminary examination of specimens indicates that these molt patterns are not found in other species in the order Piciformes, including barbets, toucans, and honeyguides, indicating that they evolved after ancestral woodpeckers split from these other families.



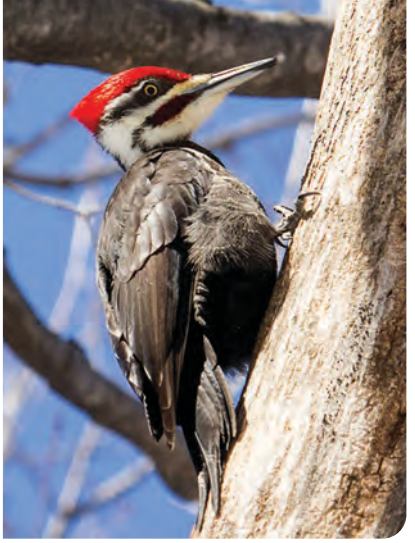


Fig. 3 (BELOW) • *Boisé Ste-Dorothée, Laval, Québec; Nov. 24, 2019. Photo by © Louise Auclair*
[macaulaylibrary.org/asset/189629961]

Fig. 4 (LEFT) • *Forêt du ruisseau Ste-Rose, Laval, Québec; Mar. 30, 2017. Photo by © Louise Auclair.*
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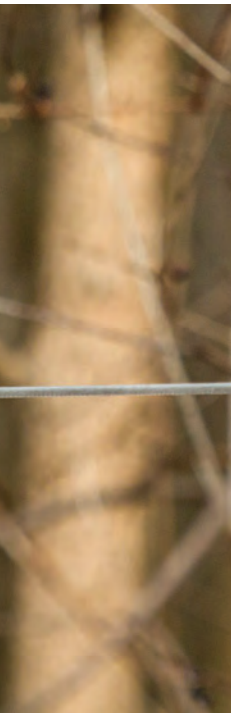
In figuring out these impelling molt patterns, Steve Howell and I examined 1,399 specimens of woodpeckers for our 1995 paper in the *Journal of Field Ornithology*. Among those were some birds with 1–2 extremely worn primary coverts among the 4–6 outermost feathers. In our analysis, we stuck our necks out and considered these to be juvenile coverts that had been retained through both the second and third prebasic molts—thus, not to be replaced until the fourth prebasic molt, at 38–40 months of age! Many of these had two generations of primary coverts to the outside of those, corresponding to coverts replaced during the second and third prebasic molts. Three years later, however, I got cold feet and advised in Part I of my *Identification Guide* (1997): "More study needed." We were already proposing methods to age woodpeckers up to their first 26–28 months of life, a radical advancement at the time. To extend this another 12 months seemed perilous, given how banders of common species like Downy and Great Spotted woodpeckers cherished their aging criteria.

This phenomenon has now been confirmed with recaptured woodpeckers. For example: work on Black-backed Woodpeckers, undertaken by the Institute for Bird Populations, reported by Rodney B. Siegel and coauthors in a 2016 paper in *The Auk: Ornithological Advances* (tinyurl.com/Siegel-Auk). This paper provides the answer to a question you might have asked yourself: What possible advantages are there in establishing such aging criteria in the first place? Well, the Black-backed Woodpecker paper shows that newly burned forests are typically colonized by first-year birds, and that they often "ride out" the burn through their lifetimes. Wood-boring beetle larvae, the favored food of Black-backed Woodpeckers, peak in abundance 3–5 years after a forest has been burned, which coincides with peak reproductive success of woodpeckers, at 3–5 years of age and breeding experience.



What Steve and I didn't find, or didn't notice, were birds that may have retained juvenile secondaries for three years. In this Pileated Woodpecker, both the fourth primary covert from the outside and s2 are worn, indicating what we now believe to be the third-basic plumage. Again, note how these juvenile feathers are even more worn than in the second basic birds (Figs. 2 & 6), being a year older. In this regard, see Fig. 7, depicting a Pileated Woodpecker that appears to have the juvenile fourth and fifth primary coverts retained, along with perhaps the juvenile second secondary (s2). Larger birds generally replace fewer feathers on average than smaller birds, so might retention of 1–2 juvenile secondaries through the fourth prebasic molt be a regular pattern in Pileated Woodpecker?

We've seen what can happen during the second and third prebasic molts in woodpeckers, but then what? In other words, what occurs after all the juvenile feathers have been replaced? Larger birds, such as hawks, eagles, pelicans, and frigatebirds, undergo a molting pattern known as Staffelmauser, or stepwise molt; see my 2006 paper in *Western Birds* (tinyurl.com/Pyle-Western-Birds) for more about this. Those birds often lack the time to replace all primaries and secondaries in one season, undergoing incomplete prebasic molts. In these large birds, as well as in woodpeckers, juvenile feathers may be retained during the second and sometimes the third prebasic molts. The cool thing about Staffelmauser is that the ensuing molt takes off in sequence where the previous molt stopped, while at the same time a new sequence begins. The result is that more than one molt "wave" occurs through these tracts, which in turn allows more feathers to be replaced per year without incurring large gaps in the wings, as would happen if adjacent feathers were replaced more rapidly.

Could this be the case with woodpeckers? To get at this question, we must first establish the replacement sequences among woodpecker primary coverts and secondaries. We might think that primary coverts in second-basic woodpeckers are replaced from the outside inwards, given that this replacement is always continuous. For example, no juvenile outer coverts seem ever to be retained, and in third-cycle birds the third and fourth coverts are newer than the outermost two. But this would be a unique strategy in birds. Might woodpeckers also replace them distally, starting with a medial covert and continuing to the outermost, matching the sequence of primary coverts of most other birds? Since so much about woodpecker molt is odd, anything is possible. This is definitely a good question for banders capturing molting woodpeckers in late summer. Secondaries are probably replaced bidirectionally from the middle tertial and proximally from the outermost feather (s1), as in almost all other bird species, but in woodpeckers it would be good to confirm this. Whatever the process, woodpeckers older than 28 months can show mixed generations of basic primary coverts and secondaries, as in the Pileated Woodpecker shown here, with s4–s7 appearing older but not being as brown and worn as would be the case if they were retained juvenile feathers.

Can we analyze crisp digital images for these questions about molt sequence? Looking closely, I see "molt clines," a gradual freshening of feathers that reflect the order in which feathers were replaced. On this bird, s10 (the middle tertial) looks slightly older than s11 (the inner tertial), and then, moving distally, s9 and s8 are progressively newer, so this part of our projected secondary replacement sequence seems to hold. We can only see the edge of s7, and it appears older than s8 but newer than s4–s6, which show a cline in the opposite direction, s6 being the oldest and s4 the newest. The outer three secondaries, s1–s3, are hard to assess, but seem newish and about equal in age. Sticking to the above replacement sequence, then, s1–s3 and s8–s11 were replaced during the previous molt, s7 and s4–s5 were replaced the year before, and s6 was replaced two molts ago. Got it? In any case, such a pattern would indicate a bird at least 40 months old, given that s6 is basic and therefore has been replaced at least once and then retained for the next two molts.

As of this writing, the Macaulay Library has 48,619 images of Pileated Woodpecker uploaded to their catalog. If you like puzzles and brainteasers like I do, go for it! I'll bet you can make some progress on confirming the replacement sequence of secondaries and, even, primary coverts in Pileated Woodpeckers. I predict that certain patterns of basic primary-covert replacement will enable the aging of some Pileated Woodpeckers up to four, or even five, years. It should then follow that you could confirm the same sequences in all other species of in the family Picidae. We can do this!

About the images

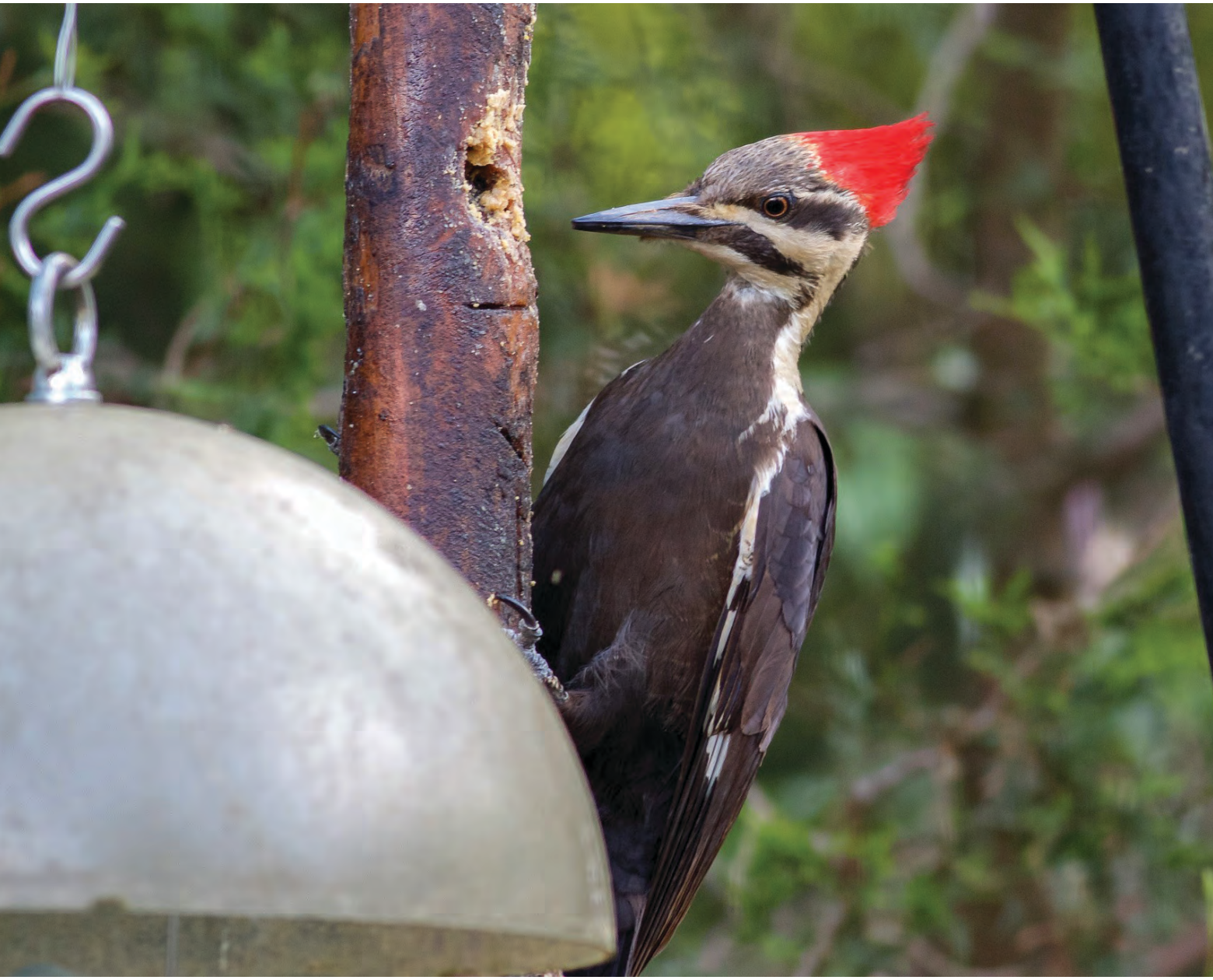
Figs. 1–4 show Pileated Woodpeckers pertaining to the four identifiable age groups. Figs. 5–8 in the expanded online content for this article show additional Pileated Woodpeckers corresponding to Figs. 1–4. The captions for Figs. 1–4 explain in detail the molt sequences and feather-retention patterns that allow these determinations; Figs. 5–8 allow the reader to begin to appreciate the variation among and within the age classes.

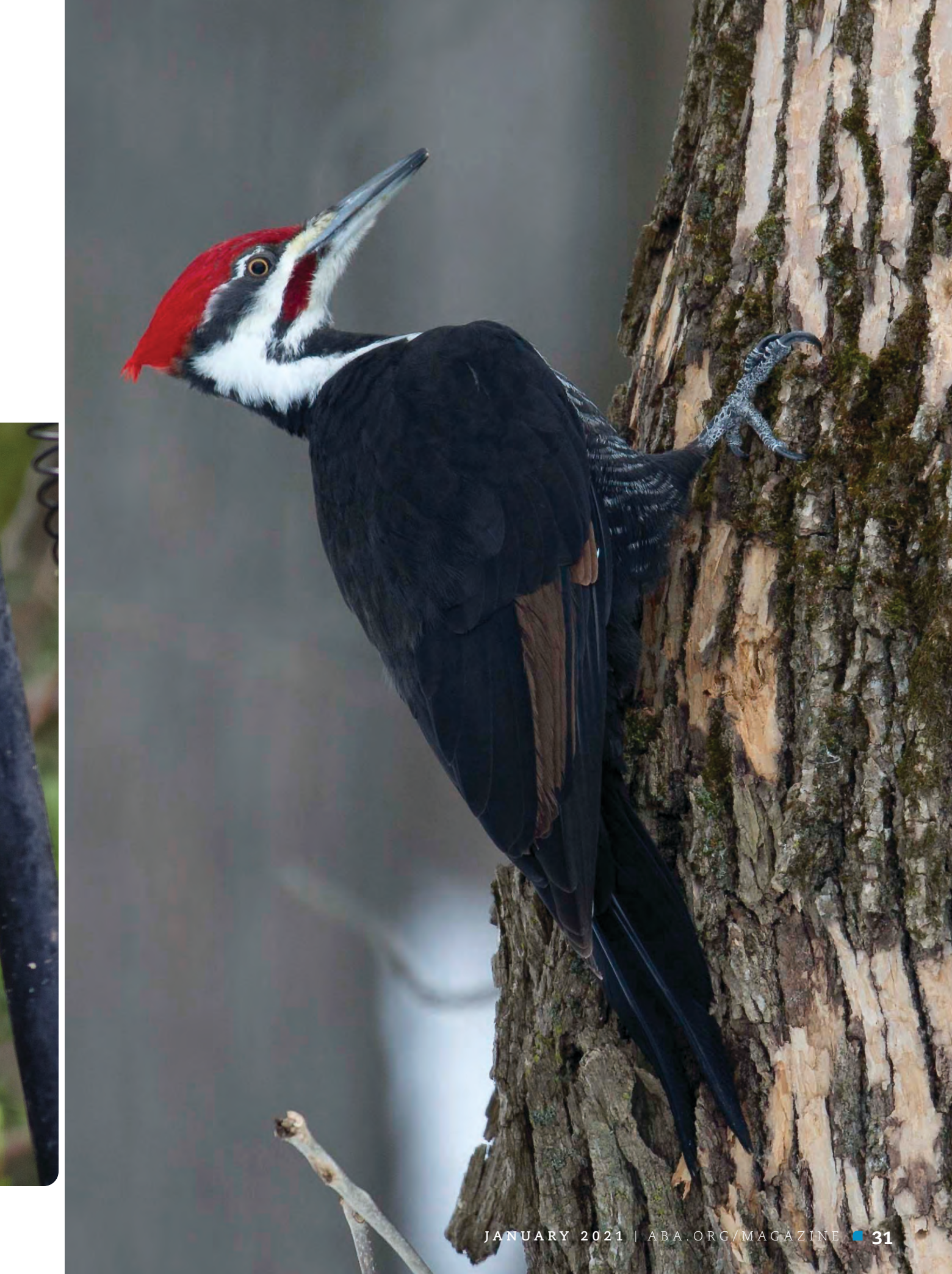
Fig. 5 (BELOW) • *Chester County, Pennsylvania; May 24, 2014. Photo by © Nick Pulcinella.* [macaulaylibrary.org/asset/61599351]

This first-cycle (formative) Pileated Woodpecker is similar to that in Fig. 1, but it shows the molt limits in the secondary coverts more explicitly. Note the blacker median coverts contrasting with the browner greater coverts. Note also that the secondaries are browner than the primaries, indicating juvenile vs. formative feathers, respectively.

Fig. 6 (RIGHT) • *Petrie Island, Ottawa, Ontario; Feb. 23, 2017. Photo by © Tom Devecseri.* [macaulaylibrary.org/asset/49465111]

This second-cycle Pileated Woodpecker has replaced the outer two primary coverts, which contrast with at least three visible juvenile primary coverts; compare with Fig. 2. Also, the bird has replaced all secondaries except s2–s6. Note the high contrast between the newer, blacker, second-basic feathers and juvenile feathers, which are now a year-and-a-half old.





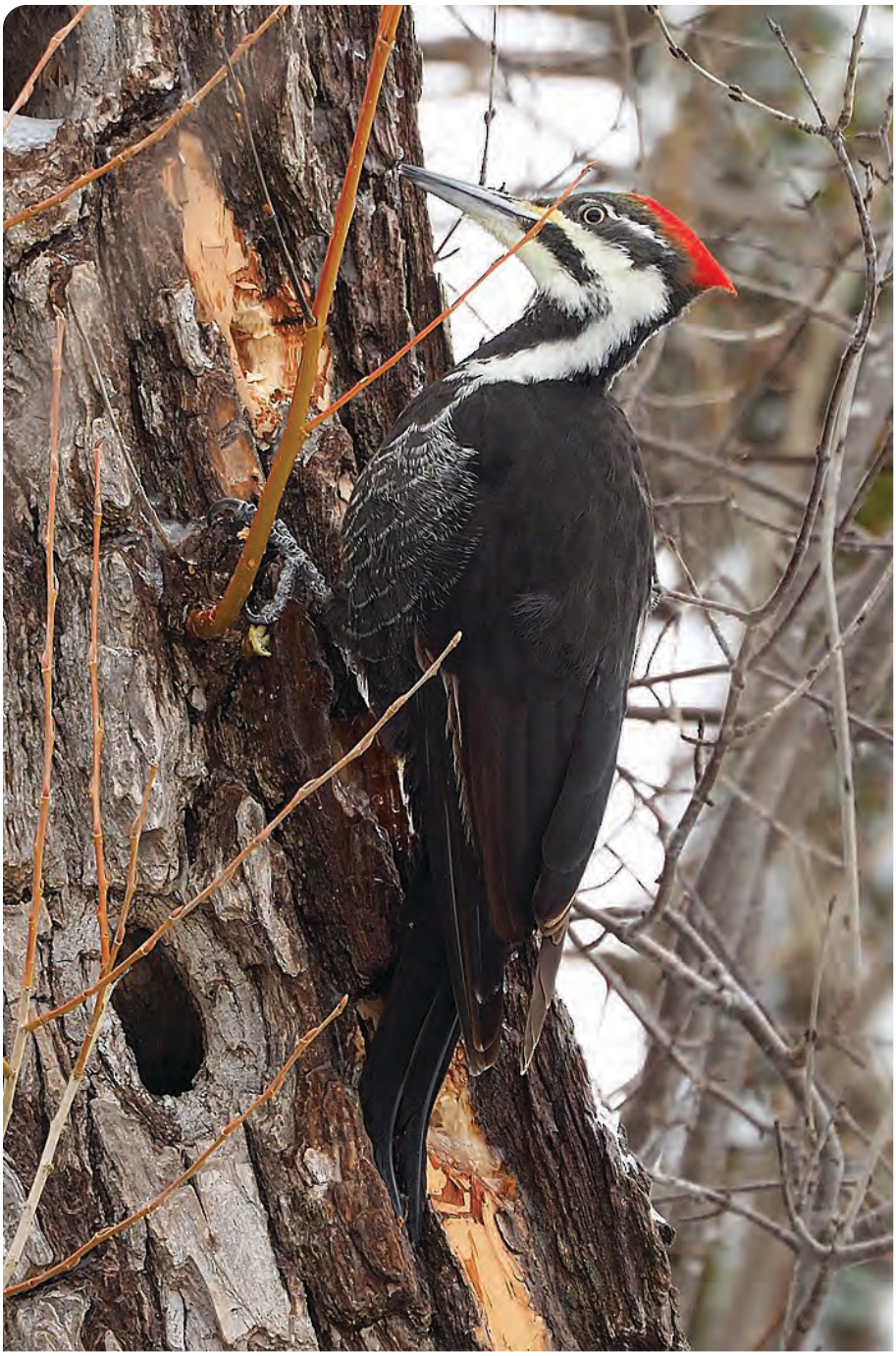


Fig. 7 (LEFT) • *Shirley's Bay, Ottawa, Ontario; Jan. 4, 2019. Photo by © Gordon Johnston.* [macaulaylibrary.org/asset/205537411]

This woodpecker is similar to the third-cycle bird shown in Fig. 3, but there are two retained juvenile primary coverts, the fourth and fifth from the outside (note that the second and third are newer than the outermost, third-basic and second-basic, respectively) and has retained two juvenile secondaries, s4–s5. As with the primary coverts, three generations are visible; note that the tertials are third-basic, newer than s6–s8, which are second-basic, which are in turn much newer than the juvenile s4–s5.

Fig. 8 (RIGHT) • *Rocky Ridge, Franklin County, Missouri; Dec. 19, 2016. Photo by © Jack and Shirley Foreman.* [macaulaylibrary.org/asset/42945721]

This bird mimics what is found in third-cycle birds (see Fig. 4), but two things make this an older bird: firstly, the retained primary coverts (fourth and fifth from the outside) are not nearly as worn as in a third-cycle bird, and thus are basic; and, secondly, the retained secondaries (s2–s3 and s5–s6), in addition to being less worn than juvenile feathers, are not consecutive. This sort of pattern indicates an older bird, but how old, at minimum?

Acknowledgments

I found these images in Cornell Lab of Ornithology's Macaulay Library catalog, which has emerged in recent years as an incredible resource for the study of bird molt. Additional images and analyses appear in the expanded digital version of this article. I thank the thousands of citizen scientists who have contributed images to the Macaulay Library and for agreeing to the license allowing use for research purposes. I especially thank the photographers who shared the images used in this article. Louise Auclair, Tom Devecseri, Jack and Shirley Foreman, Gordon Johnston, Annie Lavoie, Mason Maron, and Nick Pulcinella.