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FLIGHT-FEATHER MOLT PATTERNS AND AGE IN NORTH AMERICAN WOODPECKERS

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Abstract.—Specimens of 1399 North American woodpeckers were examined to assess flight-feather replacement patterns and their use in aging. The primaries and rectrices are fully replaced during the first prebasic molt in most species, but fully retained in two species. In contrast, all species typically retain secondaries and primary coverts during the first prebasic molt, and the regular retention of up to six secondaries during definitive prebasic molts is found in some birds of most species. Replacement of the primary coverts during the second prebasic molt is incomplete, 0–5 consecutive outer coverts typically being renewed. This delayed replacement pattern of primary coverts, not corresponding to the replacement of the primaries, may be unique in woodpeckers (and perhaps certain kingfishers) among birds. By combining retention patterns with differences in color pattern and relative wear between juvenal and adult feathers, many woodpeckers can be reliably aged through their third or fourth year of life.

PATRÓN DE MUDA DE LAS PLUMAS DE VUELO Y EDAD EN PÁJAROS CARPINTEROS DE NORTE AMÉRICA

Sinopsis.—Se examinaron 1399 especímenes de pájaros carpinteros de Norte América para determinar el patrón de reemplazo de las plumas de vuelo y su utilidad para determinar la edad. Durante la primera muda prebásica las primarias y las rectrices son reemplazadas en su totalidad en la gran mayoría de las especies y retenidas en dos de éstas. En contraste, todas las especies típicamente retienen las secundarias y las cobijas primarias durante la primera muda prebásica y algunos individuos de la mayoría de las especies retienen de forma regular hasta seis de las secundarias. El reemplazo de las cobijas primarias durante la segunda muda prebásica es incompleto, remplazándose consecutivamente de 0–5 cobijas exteriores. Este retraso en el reemplazo de las cobijas primarias, el cual no corresponde al reemplazo de las primarias, puede ser único en los carpinteros (y quizás en algunos martin pescadores). Combinando el patrón de retención de algunas plumas, las diferencias en los patrones de coloración y desgaste entre el plumaje de juvenil y el de los adultos, se podría determinar la edad de pájaros carpinteros en su tercer y cuarto año de vida.

Woodpeckers have long interested North American ornithologists researching systematics, behavioral ecology and other topics of life history (e.g., Howell 1952; Koenig and Mumme 1987; Morrison and With 1987; Selander and Giller 1966; Short 1965, 1971, 1982). It is thus surprising that so little attention has focused on molt in this group. Differences in the timing and extent of molts can lead to accurate aging of woodpeckers, a vital component to increasingly important studies on reproductive success, population ecology and conservation-related management.

Historically, a complete annual prebasic molt was assumed to occur in both juveniles and adults of most species of North American woodpeckers (Bent 1939, Forbush 1927, Howell 1952, Oberholser 1974, Stone 1896). Test (1945), Stresemann and Stresemann (1966), and George (1972) were the first to point out that the secondaries are not replaced during the first prebasic molt in certain species. George (1972) further indicated that the primary coverts typically may not be replaced during this molt, and that differences in quality between juvenile and adult feathers may be useful for aging. Work in Europe (summarized by Baker 1993, Cramp 1985, Ginn and Melville 1983) has confirmed these findings for the first prebasic molt in European woodpeckers, although details of primary covert retention remain poorly documented. In North America, however, this information has been overlooked or, at best, only vaguely recognized (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991; Jackson 1979, 1994; Rea 1970; Roberts 1955; Short 1982; Wood 1969). Test (1945) also mentioned the regular retention of some secondaries during definitive prebasic molts of adult flickers (*Colaptes*), an aspect of woodpecker molt that subsequently has been overlooked almost entirely in both the European and North American literature.

To understand further molt and its applicability to aging North American woodpeckers, we examined specimens of all 21 extant species occurring north of Mexico for information on the timing and extent of molts, and the occurrence and sequence of retained flight feathers. Here we report our findings, and their usefulness for precise aging. We propose that many birds can be reliably aged up to their third or fourth year of life.

METHODS

Specimens of 1399 North American woodpeckers, housed at the California Academy of Sciences (CAS), San Francisco, Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, and Point Reyes Bird Observatory (PRBO), Stinson Beach, California, were examined (Table 1). Specimen tag data, including sex, subspecies, date and location of collection, and any notations regarding age, were noted and synthesized as part of the examination. Within each species, specimens from a wide range of geographic localities and/or from all recognized subspecies (see American Ornithologists' Union 1957) were examined for intraspecific variation in molt patterns; no substantive differences due to these variables, or to sex, were detected. Flight-feather molt patterns in populations of the Yellow-bellied Sapsucker complex (*Sphyrapicus varius, S. nuchalis,* and *S. ruber*) were found to be very similar; therefore, these forms are lumped in this paper. As species in the previously recognized genus *Centurus* (American Ornithologists' Union 1957) show very different molt patterns to those of *Melanerpes,* in which they are now placed, we have recognized *Centurus* in this paper; this decision was based on practical rather than taxonomic considerations.

Terminology of molt, plumages and feather generations follows Humphrey and Parkes (1959; see also Thompson and Leu 1994). Generations of feathers and plumages subsequent to fledging are termed "juvenal," "1st basic," "2nd basic," etc., whereas "definitive" refers to feathers and plumages that are at least 1st basic in age (i.e., are not juvenal), but otherwise are of unknown age. "Adult" birds are those in definitive plumage. Birds in active molt refer to those that were showing symmetrical

TABLE 1. Sample sizes of 1170 North American woodpecker specimens examined, according to age-code assignment, and group categories of each species according to flight-feather replacement patterns. The three forms of Yellow-bellied Sapsuckers are here combined and we recognize the genus *Centurus* (see text). Specimens in juvenal plumage (n = 229, including at least five of each species), are not included in the table.

Species	Group	U/AHY	HY/SY	AHY/ASY	SY/TY	ASY/ATY	TY/4Y
Lewis' Woodpecker *Melanerpes lewis*	B	—	44	—	18	31	4
Red-headed Woodpecker *M. erythrocephalus*	C	—	25	6	14	22	—
Acorn Woodpecker *M. formicivorus*	B	—	28	5	10	35	—
Gila Woodpecker *Centurus uropygialis*	A	—	14	1	9	20	—
Golden-fronted Woodpecker *C. aurifrons*	A	—	20	—	10	16	—
Red-bellied Woodpecker *C. carolinus*	A	—	30	1	12	30	—
Yellow-bellied Sapsuckers *Sphyrapicus varius* group	B	—	42	—	17	30	7
Williamson's Sapsucker *S. thyroideus*	A	3	15	—	8	20	—
Ladder-backed Woodpecker *Picoides scalaris*	A	—	16	2	7	10	—
Nuttall's Woodpecker *P. nuttallii*	A	1	23	1	10	14	—
Downy Woodpecker *P. pubescens*	A	3	38	2	24	35	—
Hairy Woodpecker *P. villosus*	A	1	37	1	25	35	—
Strickland's Woodpecker *P. stricklandi*	A	4	10	—	9	23	—
Red-cockaded Woodpecker *P. borealis*	A	—	13	2	6	11	—
White-headed Woodpecker *P. albolarvatus*	A	2	25	—	16	27	1
Three-toed Woodpecker *P. tridactylus*	A	—	14	—	6	8	—
Black-backed Woodpecker *P. arcticus*	A	—	12	—	8	9	1
Northern Flicker *Colaptes auratus*	A	2	31	3	21	37	1
Pileated Woodpecker *Dryocopus pileatus*	A	—	12	—	5	18	1

replacement when collected, as indicated by missing, growing, or ensheathed feathers.

On each specimen the flight feathers, here defined as the primaries, primary coverts, secondaries (including the tertials) and rectrices, were carefully examined (see Rohwer 1971). Evidence of incomplete replacement and differences in color pattern, shape and/or wear between juvenal and definitive feathers were recorded. Birds that were collected in active molt were noted, and for other specimens, all retained flight feathers were aged and recorded by wing and position. For primary coverts, only the outer six feathers were analyzed as examination of the inner coverts could not always be performed without risking damage to the specimens.

By synthesizing all flight-feather information, each woodpecker was assigned an age code following the calendar-based system of the Bird Banding Laboratory (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991) as modified by Pyle et al. (1987). Codes included: "U/AHY" for a bird of unknown age; "HY/SY" and "AHY/ASY" for birds in and beyond their 1st basic plumage, respectively; and "SY/TY" and "ASY/ATY" for birds in and beyond their 2nd basic plumage. Here, "TY/4Y" and "ATY/A4Y" are used for birds in and beyond their 3rd basic plumage, and "4Y/5Y" indicate individuals in their 4th basic plumage. In each case the codes represent birds in the 1-yr period between completion of molts (usually October–September); the code before the slash applies until the end of the calendar year (31 December) and the code after the slash applies between the beginning of the year (1 January) and the next molt. Juveniles, here defined as birds with juvenal body plumage that were collected before the migratory period (October), were also examined. Primaries (p1–p10) and rectrices (r1–r6) were numbered distally (outward or away from the body) and secondaries (s1–s11) proximally (inward or toward the body). Data on feather replacement and measurements for statistical tests were taken from the right wing, although both wings of all specimens were examined to assess age.

Little confirmed information on flight-feather molt patterns and aging criteria in woodpeckers has been published on which to base age-code determinations of examined specimens. Indications of age on specimen labels coincided with age-code determinations in virtually all cases; however, it should be noted that, except for juveniles, the ages of the woodpeckers were inferred rather than absolutely known. Although we present substantial evidence that our age code assignments are correct, confirmation of this information through study of captive or recaptured, known-aged birds is desirable.

RESULTS AND DISCUSSION

Both juvenile and adult woodpeckers have a single annual molt that usually occurs in the late summer and fall. In migratory species the molt can be suspended or protracted, active replacement continuing until the following winter, spring or summer. Most woodpeckers follow the same sequence of flight-feather replacement. Replacement of the primaries starts with the innermost, p1, and continues in sequence to the outermost, p10. Replacement of the secondaries usually proceeds both distally and proximally from s8. In many individuals a second series of replacement proceeds proximally from the outermost secondary, s1, such that the last secondaries replaced are often s3 and s4; however, just as regularly, this second sequence seems not to occur and the outermost feather (s1) is the last replaced. Replacement of rectrices usually proceeds distally from r2 to r5 (r6 being rudimentary in woodpeckers), after which the central pair is molted (see Short 1982). Whereas the sequence is fairly invariable, the extent of flight-feather replacement during the 1st and subsequent prebasic molts shows wide interspecific variation. On the basis of this variation we have categorized North American species into three groups (A–C; Table 1).

Molt of the primaries and rectrices in North American Woodpeckers.—As has been well-documented (Chapin 1921, Cramp 1985, Sibley 1957), the first molt of primaries in many woodpeckers begins in the nest with the replacement of the minute juvenal p1–p2, and proceeds until all primaries are replaced, usually within 3–4 mo after fledging. In North America this is the rule among species of Group A, including all woodpeckers of the genera *Centurus, Picoides, Colaptes* and *Dryocopus,* and Williamson's Sapsucker (see Table 1 for English and scientific nomenclature of species examined). All HY/SY birds of Group A species examined were undergoing or had undergone a complete primary molt during the first fall, with the exception of three of 30 HY/SY Red-bellied Woodpeckers. On these, the outermost two (MVZ164337), three (CAS75999) or four (MVZ84021) juvenal primaries had been retained through the first winter or summer, indicating that a small percentage of Red-bellied Woodpeckers retain outer primaries until their 2nd prebasic molt. The juvenal outermost primary (p10) in all species of Group A was confirmed to be larger and broader than in adults (see George 1972, Jackson 1979) and this difference provides a method for separating HY from AHY birds until this feather is dropped, usually in August, September or October. Definitive molt of primaries typically was completed in August–September.

Yellow-bellied Sapsuckers also molt all of their primaries during the 1st prebasic molt, although in contrast to species of Group A, all feathers are renewed by mid-summer, well before the juvenal body plumage has been replaced. As with Group A species, the innermost primaries are reduced and the juvenal p10 is larger than the definitive p10. In the other two species of Group B, however, we found that the innermost primaries are full-sized and that all primaries are typically retained until the 2nd prebasic molt. This result confirms published information on molt in the Acorn Woodpecker (Bent 1939, Spray and MacRoberts 1975, Troetschler 1974) but contradicts that indicating more extensive or complete 1st prebasic molts in Lewis' Woodpecker (Bock 1970). We found no evidence of active, regular or symmetrical primary replacement in 121 examined juveniles and HY/SYs of these species (see Table 1), including many (>30)

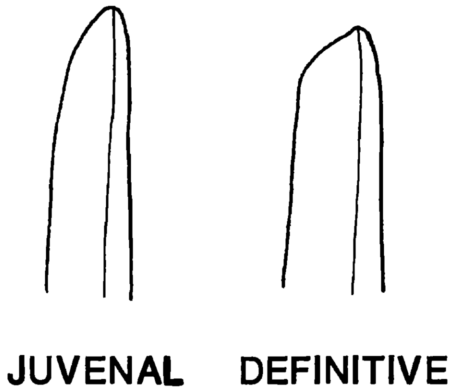

FIGURE 1. Differences in shape of juvenal and definitive outer primaries (p6–p9) in woodpeckers.

birds exhibiting active body molt. We also noted in these two species that the shape of the outer primaries (especially p6–p9) is blunter at the tip in definitive feathers and more tapered in juvenal feathers, as was found in Acorn Woodpeckers by Koenig (1980; see Fig. 1). Interestingly, the shape and size of the reduced outer primary, although showing a fair degree of individual variation, differed little on average between definitive and juvenal feathers of Lewis' and Acorn woodpeckers; differences between these groups in the distance between the tip of p10 and the tip of the longest primary covert were non-significant in both species (ANOVA, $F_{1, 38} < 2.52$, $P > 0.124$). As with Group A species, Group B species have a complete definitive primary molt. In adult Acorn Woodpeckers and Yellow-bellied Sapsuckers all primaries typically are replaced by early fall, before migration, whereas in adult Lewis' Woodpecker primary molt was confirmed to be suspended or protracted through fall (see Bock 1970) to as late as December or, in one specimen (CAS58941, assuming that the labeled date of collection is correct), 8 February. A few specimens of Acorn Woodpecker (e.g., CAS75901 and CAS75902), collected in late fall or early winter, appeared to have extremely worn juvenal outer primaries that may have been retained during the 2nd prebasic molt; more study is needed on this possible retention pattern.

The first molt of the rectrices parallels molt of primaries in these woodpeckers, i.e., all rectrices typically are replaced in Group A species and Yellow-bellied Sapsuckers, whereas all typically are retained in Lewis' and Acorn woodpeckers. In both groups the shape of the rectrices differed between juvenal and definitive feathers, being more pointed and averaging narrower in juveniles (Fig. 2), and this difference was helpful for distinguishing HY/SYs from AHY/ASYs of Lewis' and Acorn woodpeckers. Replacement of the rectrices during definitive molts typically appears to be complete in Group A and B woodpeckers, although some rectrices may occasionally be retained in Group B species.

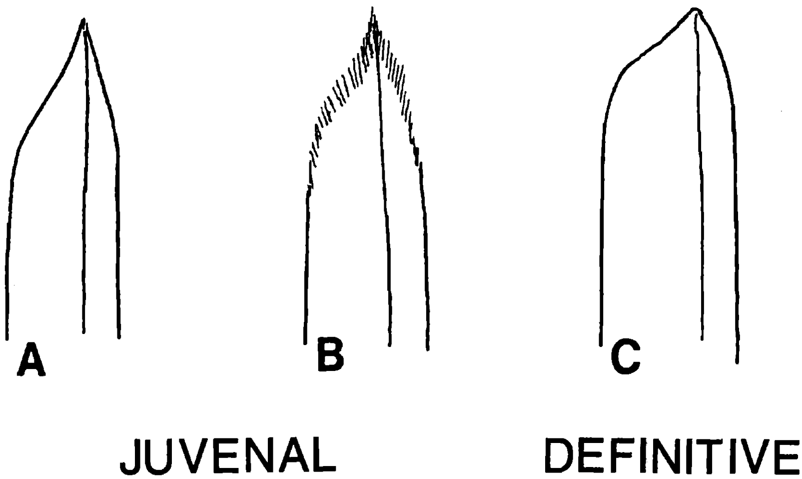

FIGURE 2. Differences in shape and condition of fresh juvenal (A), worn juvenal (B) and definitive (C) rectrices in woodpeckers. Rectrices resmbling that of figure B are found in Group B species in spring.

In the Red-headed Woodpecker ("group" C), replacement of primaries and rectrices during the 1st prebasic molt was found to be protracted and variable. Eight specimens of HY/SY birds exhibited active molt among primaries through the winter and early spring, as late as 28 March (CAS16519). The first primary molt also can be incomplete: of 13 SY birds collected in the first spring/summer (after completion of active molting), five (e.g., CAS45507, MVZ98509) had retained 1–5 outer primaries showing age-specific differences in shape, as was found in Lewis' and Acorn woodpeckers (Fig. 1). As with the latter two species, the juvenal and definitive p10 also showed non-significant differences in size in Red-headed Woodpeckers (ANOVA, $F_{1,38} = 2.11$, $P = 0.154$). Adults have a complete molt of primaries that usually finishes by fall, but that could be suspended during migration. The extent of rectrix replacement was found to be highly variable, ranging from none to (rarely) all feathers during the 1st prebasic molt and most to (usually) all feathers during definitive molts. Differences in shape between juvenal and definitive rectrices, as in other woodpeckers, are useful for aging (Fig. 2).

Retention of juvenal and definitive secondaries.—With the exception of Red-headed Woodpecker (see below), we confirmed that at least most of the juvenal secondaries typically are retained during the 1st prebasic molt in North American woodpeckers. Most individuals of Group A species retain all secondaries during this molt (Table 2; Fig. 3A), but a variable (by species) proportion can replace 1–4 (rarely to seven) inner secondaries among s7–s10 (rarely s5–s11), following the sequence noted above, i.e., s8 only, or s8–s9, s7–s9, etc., if more than one secondary is replaced (Fig. 3B). In species of *Picoides* the proportion of examined HY/SYs with

TABLE 2. Numbers of secondaries (ss) and primary coverts (pp covs) replaced or retained during prebasic molts in woodpeckers. Proportion of individuals replacing/retaining feathers and, of those doing so, the range (mean) in number of feathers replaced/retained are given. Except for number of secondaries replaced during the 1st prebasic molt (see text) species of the genera *Centurus* and *Picoides* showed very similar replacement patterns and are pooled in this table. Sample sizes and nomenclature of species examined can be found in Table 1 (see text); 52 birds collected in active secondary or primary covert molt are excluded from summary statistics.

	1st prebasic (HY/SYs)	2nd prebasic (SY/TYs)		3rd+ prebasic (ASY/ATYs)
	No. ss replaced	No. pp covs replaced	No. ss retained	No. ss retained
Group A				
Centurus species	0.36	1.00	0.02	0.02
	1–6 (2.2)	1–5 (2.4)	2 (2.0)	1 (1.0)
Williamson's Sapsucker	0.27	1.00	0.88	0.20
	4–5 (4.3)	1–4 (2.4)	1–5 (2.7)	1–4 (2.3)
Picoides species	0.07	1.00	0.30	0.25
	1–5 (1.9)	1–5 (3.4)	1–6 (2.5)	1–5 (2.0)
Northern Flicker	0.10	1.00	0.24	0.18
	2–3 (2.7)	1–5 (2.9)	1–2 (1.4)	1–3 (1.7)
Pileated Woodpecker	0.17	1.00	0.40	0.38
	1–2 (1.5)	2–4 (2.6)	1–4 (2.5)	1–5 (2.2)
Group B				
Lewis' Woodpecker	0.00	0.72	1.00	0.51
	—	1–3 (1.5)	2–6 (3.8)	1–5 (2.9)
Acorn Woodpecker	0.00	0.50	1.00	0.42
	—	1–3 (1.8)	1–6 (3.2)	1–6 (3.0)
Yellow-bellied Sapsuckers	0.00	0.42	1.00	0.68
	—	1–2 (1.3)	1–6 (3.6)	1–6 (2.9)
Group C				
Red-headed Woodpecker	1.00	0.86	0.21	0.00
	3–11 (7.5)	1–3 (1.6)	2–5 (3.3)	—

replaced inner secondaries varied from none in Hairy, White-headed, Three-toed, and Black-backed Woodpeckers (see Table 1 for sample sizes), to 31% in Ladder-backed Woodpecker. Proportions in other *Picoides* woodpeckers were: Nuttall's (17%), Downy (13%), Strickland's (10%) and Red-cockaded Woodpecker (8%). In species of *Centurus* the proportions varied from 26% in Red-bellied to 30% in Golden-fronted to 71% in Gila Woodpecker. Species of more open or xeric habitat had higher proportions of individuals with replaced inner secondaries than those typically inhabiting forested or temperate habitats (see Willoughby 1991). Species of Group B typically retain all secondaries during the 1st prebasic molt (Table 2).

No substantive differences in shape or color pattern could be detected between juvenal and definitive secondaries of Group A and B species, except that in Lewis' Woodpeckers juvenal secondaries were noticeably

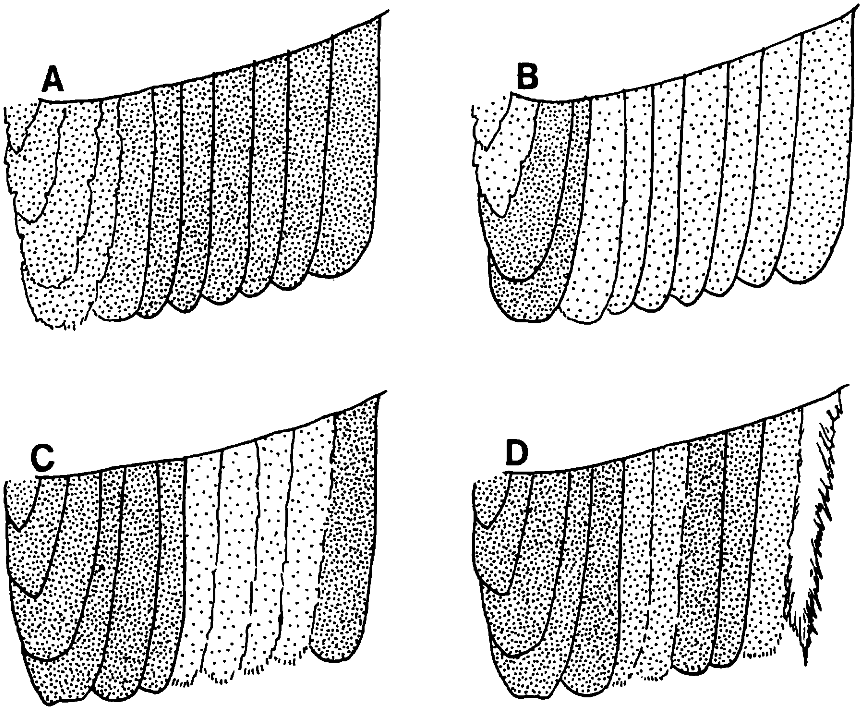

FIGURE 3. Patterns of retained secondaries in woodpeckers. A: HY/SY in spring without replaced feathers; note that the relatively exposed inner secondaries (tertials) appear more worn than in AHY/ASYs due to the juvenal feathers being of lower integrity than adult feathers. B: HY/SY of Group A species with replaced inner 1st basic secondaries, in this case, s8–s9. C: SY/TY with retained juvenal secondaries (s2–s5); note that these feathers contrast markedly in wear with replaced 1st basic feathers. D: TY/4Y of Groups B and C species with three generations of secondaries, including one retained juvenal feather (s1) and three retained, 1st basic feathers (s2, s5 and s6). Pattern D without the juvenal feather is typical of ASY/ATYs of all species; note that retained definitive feathers contrast only slightly in wear with replaced definitive feathers. See text for individual variation in retention patterns.

narrower than definitive secondaries, even when newly replaced. This difference was confirmed by measurements of the width of s6 (10 mm proximal to the feather tip): juvenal feathers averaged 20.95 mm (range 18–23), adult feathers averaged 23.55 mm (21–26), and this difference was significant (ANOVA, $F_{1,\ 38} = 36.75$, $P < 0.001$). As was suggested by George (1972), the structural integrity of juvenal secondaries appeared to be lower than that of definitive secondaries, perhaps due to lower barb densities in the former. This resulted in juvenal secondaries becoming relatively more faded and worn. By January through July, SYs usually have very worn inner secondaries (Fig. 3A), often with the white areas (if present in a given species) worn away, whereas definitive secondaries of adults

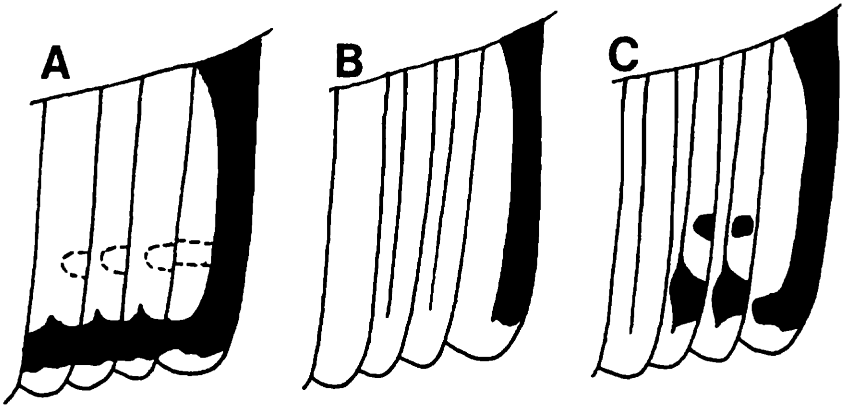

FIGURE 4. Color patterns of secondaries in Red-headed Woodpecker. A: Typical juvenile; all secondaries (s1–s11) show a full bar and in some birds a second black area occurs (indicated by the dashed lines). B: Typical adult s2–s11. C: A variation found in s2–s3 on some adults, perhaps typical of 2nd basic feathers; note that the black subterminal mark does not form a full bar. Many HY/SY Red-headed Woodpeckers retain consecutive inner secondaries (up to nine) until the second prebasic molt, the occurrence of a bar across these feathers allowing easy aging.

are relatively dark, fresh (see Fig. 3C), and with the white areas intact (see also Jackson 1994).

Red-headed Woodpeckers differed from the other species in that three to apparently all juvenal secondaries can be replaced during the 1st prebasic molt (Table 2); the last secondary replaced is typically the outermost (s1). One specimen (MVZ107060) had a single juvenal secondary (the outermost) retained on the left wing and uniform definitive feathers on the right wing, and several specimens had retained just one juvenal secondary on each wing, including one bird (MVZ98511) that still retained juvenal body feathers and was obviously in its first year. In addition, six specimens (aged AHY/ASY; Table 1) had uniform definitive secondaries but primary covert patterns consistent with HY/SYs (or possibly SY/TYs; see below). This evidence strongly suggests that some birds do replace all secondaries during the highly variable 1st prebasic molt of this species. Also, unlike other woodpeckers, the color pattern of juvenal and definitive secondaries, especially s4–s11, differs markedly (Fig. 4), which provides a useful aging criterion. One specimen (CAS22723), aged TY based on primary covert patterns (see below), had fresh definitive secondaries s1–s3 on the right wing and s3 on the left wing that were patterned like those of juveniles; whether retention of juvenal characteristics is anomalous or, perhaps, characteristic of SY/TYs awaits further study.

As documented by Test (1945), AHY/ASY Northern Flickers regularly retain some secondaries during definitive prebasic molts, and we found such retention to be true in at least a small percentage of birds in most North American species (Table 2). Higher proportions of individuals of

Group B species retain secondaries than those of Groups A and C (Table 2). In species of Groups A and B, juvenal secondaries retained by SY/TYs during the 2nd prebasic molt were very worn, contrasting greatly with replaced 2nd basic secondaries (Fig. 3C). Retained definitive secondaries of ASY/ATYs, although more worn than newly-replaced definitive secondaries, contrast less with these feathers in color, wear and shape (Fig. 3D); this difference in relative contrast can be used to distinguish age groups. Also, as noted by Test (1945), retained juvenal feathers in SY/TYs result from an arrested normal molt sequence. Thus it is often s3 and/or s4, s2–s5, s1–s6 or a series of consecutive feathers within these blocks (e.g., Fig. 3C), that are retained, although in many individuals consecutive, outermost juvenal secondaries (e.g., s1, s1–s2, s1–s3, etc.) can be retained. Retention of juvenal secondaries by SY/TYs is usually symmetrical in both wings, or nearly so. ASY/ATYs averaged fewer definitive secondaries retained (Table 2), and these were not always in the same patterns noted above for SY/TYs (Fig. 3D), less frequently showing symmetrical patterns. Evidence suggested that secondary replacement during definitive prebasic molts sometimes (but not always) starts with retained juvenal or definitive feathers from the year before (if any), which results in a variety of feather retention patterns. Some ASY/ATYs that had not retained feathers during the previous molt, however, might show secondary retention patterns similar to those of SY/TYs. With practice, however, most SY/TYs can readily be separated from ASY/ATYs by the relative contrasts of retained and replaced feathers, the positions of the retained feathers, and the relative symmetry in the wings of replacement patterns.

A few birds of Groups B and C (e.g., Lewis' Woodpecker CAS45612, Red-headed Woodpecker CAS58933, and Yellow-bellied Sapsucker CAS71958) had retained one or more, very abraded, juvenal secondaries among s1–s5, probably during the 3rd prebasic molt, and thus had three generations of secondaries (Fig. 3D). Along with appropriate primary covert patterns (see below) we tentatively aged the Red-headed Woodpeckers SY/TY and the others TY/4Y. No Acorn Woodpecker specimens were found with this pattern, although it might be expected.

Arrested molt patterns in the primary coverts.—The extent of primary covert replacement during the 1st and subsequent prebasic molts appears to be similar in all species of North American woodpeckers (Table 2). Like the secondaries, juvenal primary coverts became faded and abraded relative to definitive coverts, especially in spring (Figs. 5A, B). The European literature (Cramp 1985, Ginn and Melville 1983; although see Baker 1993) suggests that replacement of the primary coverts during the 1st prebasic molt typically is incomplete to complete in woodpeckers. However, we found that, except for replacement of the reduced, outermost covert in a small percentage of birds (1.3% of HY/SYs within Groups A and C only, all of which had replaced inner secondaries), all primary coverts are usually retained during this molt. None of 121 HY/SYs that exhibited active primary replacement displayed active replacement among the 2nd–6th primary coverts. Almost all specimens that were aged

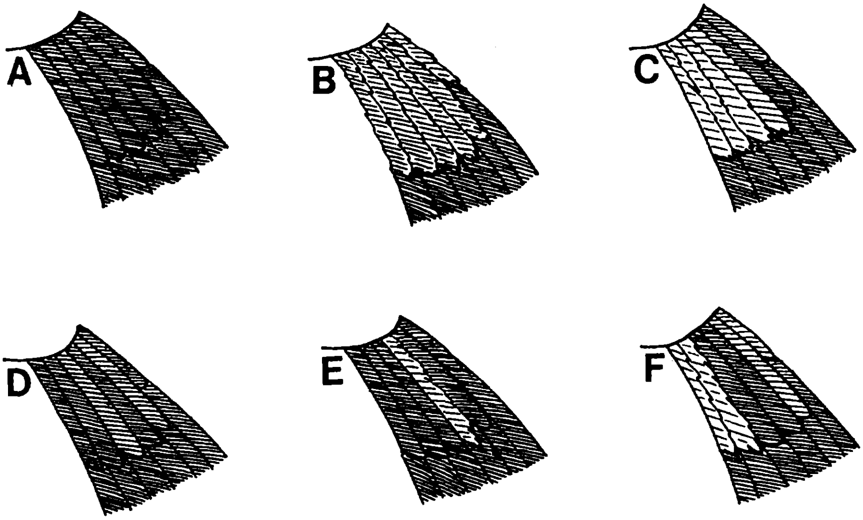

FIGURE 5. Patterns of primary covert replacement in woodpeckers. A: Fresh autumn HY/SY, or ASY/ATY with complete replacement. B: HY/SY of all groups in spring, or SY/TY in some Group B individuals. C: SY/TY in all groups, or TY/4Y in some Group B individuals, showing consecutive replacement of outer coverts. Note the high contrast between retained juvenal and replaced 2nd basic feathers. D: ASY/ATY with incomplete replacement; note that feather positions are irregular and that retained definitive coverts contrast less in wear with replaced coverts than in SY/TYs. E: ASY/ATY with isolated, retained juvenal feather, a pattern possibly indicating TY/4Y. F: Pattern typical of some TY/4Ys of Groups A and B, with three generations of coverts, juvenal (inner two feathers), 1st basic (outer two feathers) and 2nd basic (center two feathers). In all cases, outer feathers wear more rapidly than inner feathers due to increased exposure, and this should not be confused with patterns of retention. See text for individual variation in retention patterns.

HY/SY according to primary and secondary characteristics, furthermore, had uniformly brown and worn primary coverts whereas, except for some birds in Group B (see below), almost all birds aged AHY/ASY did not have uniformly brown coverts. This difference was highly significant ($\chi^2 = 884.6$, $P < 0.0001$, $n = 1092$).

We found, furthermore, that only 0–5 consecutive outer primary coverts are typically replaced during the 2nd prebasic molt, and that the contrast between these and adjacent juvenal inner primary coverts (Fig. 5C) is a reliable indicator of age SY/TY in all species. Again, almost all specimens showing the mixed juvenal and definitive secondaries of SY/TYs (see above) also showed consistent partial replacement of the outer primary coverts on both wings, either symmetrically or differing in number by one feather. This correlation between replacement patterns of the secondaries and primary coverts among SY/TYs differed significantly from a similar comparison in ASY/ATYs ($\chi^2 = 478.7$, $P < 0.0001$, $n = 600$). Evidence from birds in active 2nd prebasic molt also supported this pattern, e.g., Gila Woodpecker CAS29885, nearing completion of this molt, was replacing on each wing p8, s5, and the 2nd primary covert from the outside, the adjacent, inner four coverts being worn juvenal feathers. Similar active molting patterns were found in other woodpeckers, e.g., Hairy Woodpecker CAS45119, Black-backed Woodpecker CAS35008, and Pileated Woodpecker CAS20171. Replacement patterns on these specimens suggest that the outer coverts are renewed along with their corresponding primaries (i.e., distally), although further study on molting birds is needed.

The average number of outer primary coverts replaced during the 2nd prebasic molt varies among species, and is fewer in Group B than in the other groups (Table 2); however, this replacement pattern is fairly similar in all North American species. It is possible that a complete second molt of primary coverts may occur in some individuals of Group A species, but the distribution of replacement patterns suggests that this is rare at best, i.e., very few birds replace as many as five feathers (2.1% of SY/TYs in Table 1). This delayed replacement pattern of the primary coverts, not coinciding with corresponding primaries and taking up to two or more years to occur, may be unique among birds, although a similar pattern may exist in certain kingfishers (Pyle 1995).

A small percentage of SY/TY Lewis' (e.g., CAS35047), Red-headed (e.g., MVZ98510), and Acorn (e.g., CAS45553) woodpeckers, and many Yellow-bellied Sapsuckers (see Table 2) apparently retain all primary coverts during the 2nd prebasic molt, having uniformly very abraded and brown coverts and mixed definitive and juvenal secondaries. This pattern of retention was also found in Yellow-bellied Sapsuckers by Cramp (1985), although in that study it was mistakenly assumed that birds showing it were SYs that had replaced secondaries during the first spring. Of winter and spring (December–June) Yellow-bellied Sapsuckers examined by us, none of 59 birds (29 HY/SYs and 30 AHY/ASYs) showed active replacement of secondaries. In Group A birds, the distribution of covert replacement patterns (i.e., only 9.7% of SY/TYs had replaced just one covert), suggests that retention of all juvenal coverts during the 2nd prebasic molt is rare in these species. As we did not examine the inner primary coverts we do not know when these are replaced, but data from a few specimens (e.g., Lewis' Woodpecker CAS45600, Gila Woodpecker CAS29883 and Red-cockaded Woodpecker MVZ84201), plus data on Great Spotted Woodpecker (*Picoides major*) presented by Ginn and Melville (1983) suggest that the innermost coverts can also be replaced during the 2nd prebasic molt, resulting in the central coverts (5th–7th from the outside) being the last replaced.

ASY/ATY woodpeckers replace either all or most primary coverts (Table 2), resulting in retention patterns that differ from those of SY/TYs (Fig. 5D) and are less frequently symmetrical. We found 24 specimens of 14 species (e.g., Acorn Woodpecker CAS39318, Golden-fronted Woodpecker MVZ126113, Hairy Woodpecker CAS76206, and Pileated Woodpecker CAS31853) with what appeared to be one or two isolated juvenal coverts, usually among the 2nd–5th from the outside, that had been retained among one or more generations of definitive feathers (Fig. 5E). We did not assign precise age codes to these birds, but suspect that some of them may have been TY/4Ys or 4Y/5Ys. Alternatively, replacement of coverts during the 2nd prebasic molt may not always occur consecutively among the outside (and/or inside) feathers. On other specimens (e.g., Lewis' Woodpecker CAS45612, Downy Woodpecker CAS21018, Black-backed Woodpecker CAS29305, and Northern Flicker CAS45740), three generations of coverts were present, with the outer 1–3 appearing to be 1st basic feathers, the adjacent 1–2 coverts being newly replaced 2nd basic feathers, and subsequent inner coverts appearing to be juvenal (Fig. 5F). Along with consistent replacement patterns among secondaries (see above) we tentatively aged these TY/4Y or, in a few individuals of the Yellow-bellied Sapsucker complex (see below), 4Y/5Y.

As to aging, problematic birds include those with no or one replaced outer primary coverts, which could be either HY/SYs or SY/TYs, or birds of Group B with one to several replaced outer coverts, which could be either SY/TYs or TY/4Ys. When replacement patterns of secondaries and primary coverts were not diagnostic when combined, we chose to assign imprecise age codes (AHY/ASY or ASY/ATY in Table 1). We found that birds that had retained more secondaries had replaced significantly fewer primary coverts (linear regression using SY/TYs, $F_{1,152} = 4.4$, $P = 0.038$), so HY/SYs with one covert replaced would be expected to have replaced inner secondaries, and SY/TYs or TY/4Ys with no or few coverts replaced would also retain more juvenal or definitive secondaries (see Table 2). This difference can likely be used to help age problematic birds. Woodpeckers of Group B with mixed old and new definitive secondaries and with consecutively replaced outer primary coverts (Fig. 5C) were tentatively aged TY/4Y.

Also, we found that the uniform juvenal primary coverts in fall, when fresh, could closely resemble those of adults with uniform definitive feathers (Fig. 5A) and this resulted in a few birds (with indeterminate flight-feather characteristics, otherwise) being aged U/AHY (Table 1). More study on live, known-age birds is needed to ascertain replacement patterns of inner relative to outer primary coverts, and the relationship of retention patterns to age in woodpeckers.

Aging North American woodpeckers by molt patterns and other criteria.— By combining information on flight-feather molt patterns with other criteria, such as eye color and juvenal plumage characteristics (George 1972, Howell 1952, Jackson 1979, Koenig 1980, Short 1982, Spray and MacRoberts 1975, Wood and Wood 1973), we propose that most woodpeckers can be reliably aged through ASY/ATY and that a few individuals of certain species may be aged TY/4Y. In all cases, birds in active molt (usually in July–October but in some species through winter or spring), should be carefully assessed, older flight-feather generations usually providing more clues to precise aging than newly-replaced feathers. Birds with conflicting or anomalous characters will be found that should not be aged precisely (e.g., assigned U/AHY or AHY/ASY); only birds in which retention patterns of all flight-feather groups coincide should be precisely aged. Aging of woodpeckers in October–September is briefly summarized as follows:

In Group A species (see Table 2), HY/SYs have either uniform juvenal secondaries (Fig. 3A), or 1–4 (rarely to seven) inner feathers among s7–s10 (rarely s5–s11) 1st basic (Fig. 3B); *and* primary coverts uniformly juvenal (Figs. 5A, B) or rarely with the small outermost feather 1st basic. Some Red-bellied Woodpeckers retaining a few outer juvenal primaries through the second summer are reliably aged HY/SY. SY/TYs have either uniform definitive (2nd basic) secondaries, or secondaries with 1–6 juvenal feathers retained among s1–s6 (Fig. 3C), usually symmetrically on both wings; *and* consecutive, outer 1–5 primary coverts definitive (2nd basic), contrasting with consecutive inner primary coverts juvenal (Fig. 5C). ASY/ATYs have secondaries like those of SY/TYs except that 1–5 definitive feathers are retained among s1–s8 (see Fig. 3D), often not symmetrically on both wings, *and* primary coverts are either uniformly definitive (Fig. 5A) or irregularly mixed with retained definitive feathers (Fig. 5D). Occasional TY/4Ys of certain species may be aged by having secondary patterns as in ASY/ATYs *and* three generations of primary coverts as shown in Figure 5F.

In Group B species (Table 2), HY/SYs retain all juvenal flight feathers (except primaries and rectrices in Yellow-bellied Sapsuckers), juvenal primaries and rectrices being tapered or pointed (Figs. 1, 2A) and juvenal secondaries and primary coverts uniformly worn (Figs. 3A, 5A, B). Some or most juvenal body plumage is often retained through early winter or, in Yellow-bellied Sapsucker (*S. varius* only), first summer. SY/TYs have definitive (2nd basic) primaries and rectrices (Figs. 1, 2C); secondaries mixed, with 1–6 juvenal feathers retained among s1–s6 (Fig. 3C), usually symmetrically on both wings; *and* primary coverts either uniform juvenal and abraded (Fig. 5B), or with 1–3 outer feathers definitive (Fig. 5C). ASY/ATYs are like SY/TYs except that secondaries are either uniformly definitive or contain 1–6 retained definitive feathers among s1–s8 (see Fig. 3D), usually not symmetrically on both wings; *and* primary coverts either uniformly definitive (Fig. 5A) or irregularly mixed with retained definitive feathers (Fig. 5D). Some TY/4Ys can probably be reliably aged, having three generations of secondaries including one or more very abraded juvenal feathers (Fig. 3D); *and* two or three generations of primary coverts, with replacement patterns as shown in Figure 3D or 3F.

In Red-headed Woodpeckers, HY/SYs may have flight feathers in symmetrical molt through winter or spring; 0–5 outermost juvenal primaries (Fig. 1) sometimes retained through 2nd summer; some or all juvenal rectrices (Figs. 2A, B) usually retained; 0–8 juvenal innermost secondaries retained with full subterminal blackish bands (Fig. 4A); *and* primary coverts uniformly juvenal (Figs. 5A, B), sometimes with the outermost contrastingly fresh. SY/TYs have flight feathers usually not in active molt beyond December; primaries uniformly definitive (2nd basic; Fig. 1); all or most rectrices usually definitive (2nd basic; Fig. 2C); secondaries usually uniformly definitive (2nd basic; Figs. 4B, C), or occasionally with retained 1st basic (and sometimes juvenal) feathers (see Fig. 3D); *and* primary coverts juvenal with 0–3 outer feathers 2nd basic (Figs. 5B, C). ASY/ATYs should have secondaries uniformly definitive (Figs. 4B, C), perhaps rarely with one or more, contrastingly worn, retained definitive feathers; *and* primary coverts either uniformly definitive (Fig. 5A), or irregularly mixed with retained definitive feathers (Fig. 5D).

CONCLUSIONS

Flight-feather replacement patterns in North American woodpeckers follow similar sequences among species but feather replacement varies greatly as to timing, taking 1–2 yr for all juvenal primaries to be replaced, 1–3 yr for all juvenal secondaries to to be renewed, and 2–4 or more yr for all juvenal primary coverts to be replaced. Why replacement of these feathers occurs so slowly in relation to most other birds; whether it is due to energetics, social signalling or other factors, would be an interesting topic of study. Also of interest would be the systematic implications, if any, of molt patterns in woodpeckers.

Knowledge of these patterns and their timing, along with differences between juvenal and adult flight feathers, can be used to age woodpeckers of certain species up to their third or fourth year. In some birds, however, it may not be easy to distinguish juvenal from adult feathers without practice, or replacement patterns may conflict with what would be expected given the above information. Responsible aging always includes the willingness to place a bird in a less-precise age group should any uncertainty exist. Although we have a high degree of confidence in the feather retention patterns and aging criteria that we propose, especially given the highly significant correlations between expected patterns in different groups of flight feathers within each age class, we must again stress that most ages in this study have been inferred, primarily because (1) insufficient numbers of AHY specimens in active molt were present (only 2.4% of 699 specimens examined; see Thompson and Leu 1994) and (2) our inability to follow each molt sequence through completion using specimens. Thus, confirmation of our proposed aging criteria is needed, through study of actively-molting, known-aged, captive or marked individuals.

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