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DETERMINATION OF AGE IN THE SPOTTED TOWHEE

By JOHN DAVIS

The segregation of series of birds into age classes is of paramount importance to the avian taxonomist, physiologist, and student of bird behavior and ecology. In passerines, age groups have been shown to differ in measurements (for example, Aphelocoma, Pitelka, 1951:199; Pipilo erythrophthalmus, Sibley, 1950:115) and in physiology (Agelaius phoeniceus, Wright and Wright, 1944:49–55). Pitelka (1945:256) stated that age classes in Aphelocoma differ so widely in the measurements of structures used in taxonomy that "any work on the systematics of corvids in which first-year specimens are not distinguished from adults is at once suspect." The importance of age determination of individuals to the scientist investigating the behavior and ecology of banded birds is so obvious as to require no further comment here.

In the present study 123 males and 70 females of the Spotted Towhee (*Pipilo erythrophthalmus*) were collected over a 16-month period in order to determine the annual reproductive cycles. All birds were taken within three miles of the Hastings Reservation, northern Monterey County, California, and were members of a continuous population of the subspecies *P. e. megalonyx*. Since the skin of each bird was saved, there is available a large series representing first-year and adult birds taken in every month of the year, from which information can be derived as to the morphological differences between age groups. Most of the criteria for determining age were derived from series of 14 adult and 14 first-year males and nine adult and four first-year females, all collected in the fall and early winter when first-year individuals could be distinguished by the incompleteness of the apparent double-walling of the skull. Other criteria were established by using the entire series of males and females.

Criteria now in use.—Dwight (1900:207), working with northeastern populations of Pipilo erythrophthalmus, stated that the postjuvenal molt of this species is partial, first-year birds retaining the primaries, the primary coverts, and the secondaries. "Young and old become almost indistinguishable except by the browner primary coverts of the young birds."

Sibley (1950:114), working with western and Mexican races of *P. erythrophthal-mus*, used the contrast between the retained, brownish primary coverts and the fresh, black secondary coverts to distinguish first-year males. In adult males both the primary and the secondary coverts are black. He stated that the contrast between the two series of coverts in females was "not great enough to permit dependable age determination."

In the series at hand, the criterion of the color of the primary coverts is of great value in differentiating first-year males. Females can actually be differentiated on this character, the coverts of adults ranging from dark gray to black. However, by midwinter the primary coverts of most females have oxidized to a brownish hue that is similar to that of the coverts of first-year birds. The usefulness of this character in females thus lies chiefly within the period during which age can be determined by the degree of skull ossification, but it may be applied to fall and winter specimens for which information on skull characters is lacking.

Swarth (1905:172) stated that the rumps of first-year male *P. e. megalonyx* are grayish, whereas the rumps of adults are black. In the series at hand, the average rump color of first-year birds is paler and grayer than that of adults. However, there is considerable variation in this character within each age class, and the overlap between them is too great to permit the use of rump color as a criterion for determining age.

The specimens at hand indicate that there are other useful characters for establishing age in the Spotted Towhee. These are of particular value in connection with the ages

of females, but they serve also to corroborate the ages of males which have been classified on the basis of the color of the primary coverts. As Emlen (1936:102) has stated for *Corvus brachyrhynchos*, and Pitelka (1945:256) for *Aphelocoma*, the characters distinguishing first-year birds from adults should not be used individually, but in combination. The following characters can be combined with primary covert color to determine age.

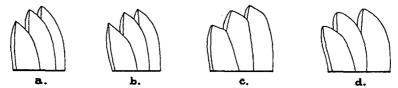


Fig. 1. Shape of lateral rectrices of *Pipilo erythrophthalmus megalonyx* collected near the Hastings Reservation, Monterey County, California. a, juvenal female, July 6, 1955; b, first-year male, September 28, 1955; c, adult male, November 26, 1955; d, adult male, December 22, 1955.

Shape of the rectrices.—The material at hand presents concrete evidence that in the great majority of first-year birds the rectrices are not lost at the postjuvenal molt. When the series of 14 known adult and 14 known first-year males are compared, two differences in the rectrices are obvious. First, the rectrices of the adults are considerably less worn. Second, the tips of the rectrices of the first-year birds are rounded or pointed, whereas those of the adults are noticeably blunt or truncate (fig. 1). The difference in shape is especially evident in the three outer rectrices, and most consistently in rectrices 4 and 5. Two first-year males are of particular interest. Number 70, collected on December 5, 1955, had evidently suffered a previous accident to its tail, as rectrices 1-6 on the right side and rectrix 1 on the left side are being replaced. The rectrices of the left side are pointed whereas those of the right side are truncate. Number 90, collected on January 26, 1956, with the skull about nine-tenths ossified, has replaced rectrices 4-6 on the right side, these feathers being much less worn than their counterparts on the left side. Rectrices 5 and 6 of the right side are pointed, but rectrix 4 is truncate. This would indicate that all replaced juvenal rectrices are not necessarily of adult configuration.

To test the value of these characters, the two series of males were intermingled and the flat skins placed in a pile. It took exactly 90 seconds to sort out the 14 immatures, without error, on the basis of shape and wear of the rectrices. The same differences in wear and configuration are evident in the rectrices of first-year and adult females.

However, the rectrices of adults are not invariably truncate (fig. 1d). The situation is similar to that described for *Aphelocoma* by Pitelka (1945:256), in which the "adult rectrices are not necessarily truncate and, indeed, may be strongly suggestive of juvenal feathers," although such similarity was found to be "comparatively rare," as it is in the series of *megalonyx*. In using this character, some confusion may arise because of rectrices adventitiously replaced by first-year birds, but such replacement is usually obvious because of its asymmetry.

The shape of the tail itself does not serve to separate age classes in the Spotted Towhee. Emlen (1936:101) found that the tails of first-year American Crows were rather square whereas those of adults were rounded. This was reflected in measurements of the difference in length between the central rectrices and the next to outermost rectrices. Pitelka (1945:255), using the same measurement, demonstrated this differ-

ence between age classes in *Aphelocoma*. In the Spotted Towhee the shape of the tail varies so widely within each age class that it is not useful in determining the age of an individual.

Table 1
Width of White Spot on Rectrix 4

	Wie	dth of W	hite Spot on R	ectrix 4		
	Age 2	Determined	l on Skull Charac	cters Only		
Age	Sex	N	Range	Mean	Standard error	Standard deviation
First-year	8	13	0.0- 7.1	3.13	± 0.55	1.98
Adult	<i>\$</i>	12	5.1-10.4	7.62	±0.46	1.58
First-year	ę	4	0.0- 2.6	1.05		
Adult	Q	9	1.9- 9.9	6.29		*******
	Age Dete	ermined on	Skull and Pluma	ige Character	rs	
in All Months						
Age	Sex	N	Range	Mean	Standard error	Standard deviation
First-year	♂	39	0.0-10.4	3.20	±0.42	2.60
Adult	₫	52	0.0-10.4	7.11	±0.25	1.84
First-year	\$	24	0.0- 5.4	1.71	±0.32	1.58
Adult	Ş	37	0.0-10.1	5.89	±0.44	2.71

The retention of the rectrices by first-year *P. e. megalonyx* differs from the situation described for the nominate race in New York (Dwight, 1900:207) and Michigan (Sutton, 1935:17–18) and indicates that there is geographic variation in the extent of the postjuvenal molt. In this species, as thus far investigated, the resident birds retain the rectrices, and the migratory form replaces them.

The failure of first-year megalonyx to molt the rectrices is also of interest as regards the intrageneric relationships in Pipilo. It has been suggested that the Brown Towhee (Pipilo fuscus) and its allies are possibly not congeneric with P. erythrophthalmus and its allies (Coues, 1866:89; Davis, 1951:10, 100-101). Most immature P. fuscus retain the rectrices through the first year, and their rectrices are noticeably more rounded and less truncate than those of adults (Davis, op. cit.:3). The interspecific variation in the extent of the postjuvenal molt is apparently bridged by at least some of the western populations of Pipilo erythrophthalmus.

Tail spotting.—First-year and adult birds of both sexes differ in the width of the white spot on rectrix 4. The spot is, on the average, much narrower in first-year birds, and in many it is either absent or reduced to a narrow streak. In making measurements, when the spots were of different widths on the left and right fourth rectrices, the wider spot was always measured, except that if a fourth rectrix had been replaced adventitiously by any first-year bird, the spot on the replaced feather was not measured.

Measurements were made initially on the adults and first-year birds the ages of which had been determined on skull characters; subsequently it was made on all birds aged by plumage and/or skull characters. The two sets of data are presented in table 1, and those pertaining to the larger series are shown graphically in figure 2. In the smaller series the means for the males of the two age groups are separated by two standard deviations. In the larger series the means for both sexes are separated by five standard errors, and the average differences between adults and first-year birds are statistically significant. Reference to figure 2 will show that the white spot was absent on rectrix 4 in only one adult male of 52 (1.9 per cent) whereas it was absent in eight first-year males of 39 (20.5 per cent). For the females, the corresponding figures are one of 37

adults (2.7 per cent) and eight of 24 immatures (33.3 per cent). In the males a rather sharp break occurs at 6 mm. Eight of 52 adults (15.4 per cent) fall below this figure, and six of 39 immatures (15.4 per cent) lie above it. In the females, the break occurs at 3 mm.; four of 37 adults (10.8 per cent) fall below this figure, and three of 24 first-year females (12.5 per cent) lie above it. It seems apparent that, while not completely reliable, this plumage character can be of considerable value in determining age.

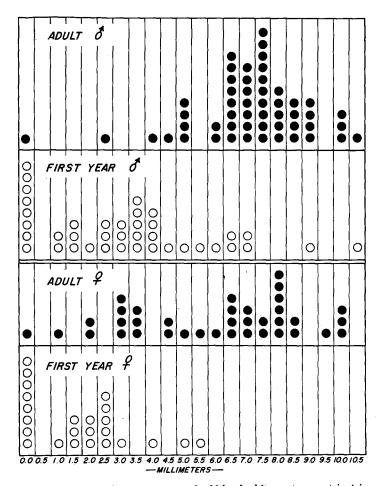


Fig. 2. Frequency of measurements of width of white spot on rectrix 4 in birds taken in all months.

Seven first-year birds have replaced rectrix 4 on one side. The measurements in millimeters of the width of the white spot on the replaced rectrix and the retained rectrix are as follows (replaced rectrix first): 6.4, 2.1; 8.7, 1.9; 7.8, 2.4; 4.8, 0.0; 5.6, 2.5; 4.0, 0.0; 0.0, 0.0. In only one of the seven birds has the replaced rectrix 4 failed to bear a larger white spot; this was in an individual lacking spots on both the new and the old feathers.

It is difficult to ascertain the adaptive significance of increased white spotting on

rectrix 4 in adults. The spot averages larger in males than in females, but the average difference is not statistically significant. Further, the increase of the white spotting in adults occurs in both sexes. These facts suggest that the spots are not used in any courtship display, and I have never seen any such display in this species. If the assumption is made that more adults than first-year birds are paired during the breeding season, as seems likely, then it may be that the white tail spots are used in threat displays in defense of territory, or as an indicator of location or position between the members of a pair. I have never seen the tail used in any threat display in a number of territorial clashes involving both sexes. However, Spotted Towhees frequently flirt the tail when hopping, and females returning to the nest often perch near it for a few seconds, flipping and flirting the tail, before going down to the eggs or young. Spotted Towhees frequently spread the tail when they take flight. Grinnell and Storer (1924:478) noted that "even then their broken pattern of coloration would be protective in effect were it not for their almost incessant activity. But when a towhee takes flight from one thicket to another its brilliant coloration flashes forth vividly; a predominance of black is seen, but the white dots on the shoulders and wings, and the white 'thumb marks' at the end of the fan-shaped spread tail, introduce a decided element of contrast." The use of the tail in these ways suggests that brief, intermittent display of the tail spots serves as an indicator of position, and this would be of importance to the members of a nesting pair, since they must frequently coordinate their movements. An increase in the extent of white tail spotting might render this signal more effective.

Wear.—The primaries, and especially the rectrices of first-year towhees are noticeably more worn than those of adults. Emlen (1936:100) noted this in Corvus brachyrhynchos and suggested that wear on the juvenal flight feathers might result in part from the severe treatment which they receive while the young are in the nest, and, possibly more important, from weaker and more brittle construction than that of the adult flight feathers. Wear during the nestling stage does not seem important in the Spotted Towhee, as the remiges and rectrices of two independent juveniles collected on June 8 and July 6 are only very slightly worn. Of great importance, however, is the chronological age of the feathers themselves. In September, when the flight feathers of the adults are fresh, such feathers have been borne for two or three months by first-year birds, and they are already worn to some degree. This differential will, of course, exist between first-year and adult birds until the following fall, when the entire plumage will be replaced by members of both groups.

As Emlen (loc. cit.) and Pitelka (1945:255) have pointed out for Corvus and Aphelocoma, respectively, differential wear is variable and is not a reliable criterion for determining age. However, Emlen found that "the occurrence of heavily worn tail feathers can be linked with first-year birds in a high percentage of cases," and Pitelka used differential wear as a means of spotting first-year Scrub Jays in the field in spring. He also found that specimens with excessively worn flight feathers were almost always first-year birds. The amount of wear on the primaries has been used as a criterion for determining age in other species (Pipilo fuscus, Davis, 1951:3–4; Passerella melodia, Marshall, 1948:240). As stated previously, differences in wear on and shape of the rectrices can be used effectively in combination to determine the ages of most specimens of the Spotted Towhee. Differential wear is of lesser value during the summer as the feathers of most individuals, regardless of age, are heavily worn by that time. However, extremely worn Spotted Towhees are almost always first-year birds as judged by other characters.

Color of the iris.—The color of the iris is grayish brown in juvenal Spotted Towhees and an intense red in adults. From the fall through the winter and early spring iris color slowly changes in first-year towhees until red irides similar to those of the adults are

acquired. The length of time over which this change takes place is variable, but most first-year birds acquire a fully red iris color by the end of May.

The first change noticeable in the grayish brown iris of the first-year bird is a suffusion of orange or reddish orange proximally, the peripheral portion retaining the juvenal color. After the peripheral portion has changed color, the iris may be pale orange, orange, reddish orange, orange red, or pale red. In a few first-year birds the irides in fall were a dull, brownish red, quite different from the vivid red of the adult iris.

Of 60 males collected between September 14 and May 25, and classed as adults on the basis of plumage and/or skull characters, 58 had red irides and two had pale irides. Of 43 first-year males collected during the same period, 37 had pale irides and six had red irides. Actually the separation might have been even more discriminating than the above figures indicate. When collecting was begun in January, 1955, I was unaware of the limits of variation of the eye color in adults and termed the eye color of all individuals regardless of age "red" unless the iris was unusually pale. As collecting progressed and more adults were examined, it became evident that the eye color of adults varied within very narrow limits and it was then possible to discriminate more accurately between the eye color of adults and first-year birds. Thus, of seven first-year males collected from January through April, 1955, the eye color of four was termed "red." In contrast, of 19 first-year males collected in the corresponding months in 1956, the eye color of only one was termed "red," that of a bird collected on April 25. The usefulness of this character should not be obscured by the initial inability to discriminate more accurately during the period of early collecting.

Of 33 adult females collected between September 14 and May 25, the eye color of all was red. Of 23 first-year females collected in the same period, the eye color of 15 was pale, and in eight it was red. Here again, the value of this character is obscured by the initial lack of familiarity with the nature of variation of the eye color of adults. Of six first-year females collected from January through April, 1955, four were assigned a "red" eye color. In the corresponding period in 1956 only one of ten first-year females was assigned a "red" eye color; this was a bird collected on March 14.

Useful though this character may be, it has obvious limitations. Very few collectors note the eye color of the Spotted Towhees which they take, and this information is lacking for the great majority of museum specimens. Further, as may be judged from what has been written previously, some familiarity with the variability of eye color is required before fine discrimination between age groups can be made. Nonetheless, bird banders could use this character to advantage after handling a number of individuals. It would also be helpful to taxonomists if museum collectors noted the presence of unusually pale eye color in specimens of Spotted Towhees.

The whole problem of iris color is simplified in the western and Mexican races of *Pipilo erythrophthalmus*, since the definitive eye color in all these races is red. The problem would be more complex in dealing with the eastern races, in which the definitive eye color may range from red through pale orange or yellow to straw. Dickinson (1952:332) has pointed out that numerous winter records of the red-eyed, migratory nominate race have been published, based on field observations of iris color. He notes that many of these records may actually pertain to one of the southern races, *P. e. canaster*, in which eye color is variable, ranging from red to pale orange, or even to yellow. Another source of error may be present in such attempts to identify subspecies through eye color alone. It may well be that the eye color of first-year *P. e. erythrophthalmus* passes through a series of orange or reddish orange stages as it changes from the brownish color in juveniles to the definitive red. If this be true, and if the transition takes as long in *erythrophthalmus* as it does in *megalonyx*, many first-year *erythrophthalmus* on the wintering

grounds would have pale irides which might resemble those of one of the southern races. If iris color changes directly from brown to red in first-year *erythrophthalmus*, this would represent a radical departure from the nature of the transition in *megalonyx*, which is probably representative of the western races in this regard.

Bursa Fabricii.—The presence of a bursa Fabricii has long been known as an indicator of age in many species of birds. In the Spotted Towhee this structure is very prominent in juveniles, but it disappears rapidly and in most individuals it is indistinguishable macroscopically by early winter. In the present series, the first male of the year without a visible bursa was collected on December 5, and the first female on January 18. Of four first-year males collected on January 26 and 27, the bursa was not visible in two, and it was present in two, measuring 4.5 and 6 mm. A bursa 3 mm. long was present in a male collected on February 1. Of four first-year males collected on February 4, a visible bursa was present in only one, measuring 2 mm. From this date on, only one first-year male, collected on March 14, had a bursa; this measured 2 mm. In the more limited series of females, a bursa was visible in first-year birds collected through December 5. A female collected on January 18 lacked a bursa and from this date on none was found. It is apparent that the bursa Fabricii is of very limited usefulness in determining age in Spotted Towhees. However, collectors should record the presence of a bursa in birds with ossified skulls, regardless of the date of collection.

SUMMARY

The following characters may be used in combination for determining age in the Spotted Towhee: (1) color of the primary coverts (of particular importance in males); (2) shape of the rectrices; (3) width of the white spot on the fourth rectrix; (4) amount of wear on the wings and tail; and (5) color of the iris.

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