

DELAYED PLUMAGE MATURATION AND THE PRESUMED PREALTERNATE MOLT IN AMERICAN REDSTARTS

SIEVERT ROHWER, WILLIAM P. KLEIN, JR., AND SCOTT HEARD

The American Redstart (*Setophaga ruticilla*) is one of about 30 sexually dichromatic North American passerine species in which males exhibit a delayed plumage maturation (Rohwer et al. 1980). Males in their first winter and in their first potential breeding season are largely like females in coloration. These young males have only a few scattered black feathers on their head, back, and breast, areas where adult males are solid black, and they have yellow rather than the orange patches characteristic of adult males in their wings and tail. Two of four hypotheses reviewed by Rohwer et al. (1980) are relevant to the delay in plumage maturation characteristic of these 30 dichromatic passerine species. Both describe hypothesized best-alternative responses by which young males have minimized their disadvantage in one or both forms of sexual competition. The first, which we here rename, is the Cryptic Hypothesis (CH). Selander (1965) developed this hypothesis by arguing that the costs of a conspicuous breeding plumage would not be repaid in yearling males because of their very limited breeding opportunities. This was called the sexual selection hypothesis by Rohwer et al. (1980) and the delayed maturation hypothesis by Procter-Gray and Holmes (1981). The second is the Female Mimicry Hypothesis (FMH). Rohwer and his coworkers (Rohwer et al. 1980, Rohwer 1983) developed this hypothesis by arguing that young males increase their chances of obtaining female-worthy territories and breeding as yearlings by mimicking females and, thus, eliciting less aggression from adult males in the early stages of territory establishment. Both hypotheses assume that breeding opportunities for young males are limited, but the FMH anticipates a substantial effort to breed by first-year males, while the CH anticipates little reproductive effort by yearling males and interprets their developed reproductive tract as a response to occasional opportunistic chances at copulation.

Past hypotheses of delayed plumage maturation have focused exclusively on adaptations relating to the breeding season (Selander 1965, Rohwer et al. 1980, Procter-Gray and Holmes 1981). Here we ask: Is the subadult plumage an adaptation to the first breeding season or is it an adaptation to the first winter season? If subadult plumages are an adaptation to the first winter season, then the major observations past workers have sought to explain are accounted for by the following three-part Winter

Adaptation Hypothesis (WAH): (1) the female-like plumage of young males is of primary (but unknown) functional importance in the first winter; (2) subadult males are simply stuck with their female-like plumage in the first potential breeding season either because they cannot afford a supplementary late winter molt or because such a specialized molt, relevant to only one age and sex class, has been difficult to evolve (see Parkes 1967); and (3) the delayed acquisition of territories by subadults (usually caused by a late spring migration) is an adaptation to reduce aggression from older males, aggression which might be particularly intense because of the inexperience and distinctive appearance of subadult males. This WAH presumes a sexual dichromatism among adults in winter, a point which is true for all of those species listed by Rohwer et al. (1980) (Table 1) as having subadult plumages in their first potential breeding season. Furthermore, the ecology and behavior of adult males and adult females must be different in winter and young males should be more similar ecologically to adult females than to adult males. This WAH would be weakened as an explanation of the breeding season occurrence of subadult plumages if, in late winter, first-year males underwent either a delayed first prebasic molt or a first prealternate molt in which new female-like feathers were grown. On the other hand, the WAH would be supported if a late winter molt produced mostly adult-male-like feathers in species in which first-winter males have a subadult plumage.

In this paper we describe in detail the prealternate molt of male American Redstarts, a species chosen for three reasons. First, redstarts are reported by Dwight (1900) to have a partial prealternate molt, but the molt itself has never been described. Second, because of this presumed molt, data on active molt for redstarts seemed potentially capable of confirming either some breeding season hypothesis (such as the CH or the FMH) or the WAH, depending on the color of actively growing feathers. Finally, relative to adult males, Rohwer et al. (1980) found subadult male redstarts to be more common in western-taken than in eastern-taken samples of museum specimens. This suggested the possibility that some yearling males in eastern populations of redstarts might acquire the definitive breeding plumage for their first (rather than their second) breeding season. Such a bimodal tactic would make good theoretical sense if, for example, early fledged young were competitively more similar to adults than late fledged young (see Rohwer et al. 1980). A bimodal maturation time for young males could be accomplished in either of two ways: first, some young males could molt directly into their definitive basic plumage in the prebasic molt, as is true for the Olive Warbler (*Peucedramus taeniatus*) (Webster 1958); second, some young males could have a complete prealternate molt, a

TABLE 1
PERCENT OF AMERICAN REDSTART SPECIMENS TAKEN ON THE WINTERING GROUNDS
THAT ARE SHOWING ACTIVE BODY MOLT

		Subadult males				Adult males				Females	
		Rictal bristles	Eyes and lores	Other contours	Total	Rictal bristles	Eyes and lores	Other contours	Total	Other contours	Total
Aug.	1-15	0	0	0	1	0	0	0	1	0	1
	16-31	0	0	0	8	0	0	0	2	0	5
Sept.	1-15	0	0	0	4	0	0	0	7	0	7
	16-30	0	0	0	7	0	18.2	0	11	37.5	8
Oct.	1-15	0	0	0	2	0	0	10.0	10	0	6
	16-31	0	0	0	8	0	8.3	0	12	0	8
Nov.	1-15	0	0	0	10	11.1	0	11.1	9	0	7
	16-30	25.0 ^a	25.0 ^a	12.5	8	0	0	0	7	20.0	5
Dec.	1-15	0	25.0	0	4	0	0	0	9	0	9
	16-31	12.5 ^a	12.5 ^a	12.5 ^a	8	0	9.1	0	11	0	5
Jan.	1-15	25.0	0	0	8	7.1 ^a	7.1 ^a	0	14	0	5
	16-31	0	0	25.0 ^a	4	0	0	0	15	13.3	15
Feb.	1-13	28.6 ^b	28.6 ^b	0	7	0	9.1	0	11	0	7
	16-28	20.0 ^a	20.0 ^a	0	5	0	7.7	0	13	0	9
Mar.	1-15	0	27.3	0	11	0	5.9 ^a	5.9 ^a	17	0	14
	16-31	7.7 ^a	7.7 ^a	0	13	0	16.7 ^a	5.6 ^a	18	3.7	27
Apr.	1-15	0	16.6 ^a	33.3 ^a	6	0	16.6	0	12	0	8
	16-30	20.0 ^a	40.0 ^a	0	10	0	14.3	0	7	0	12
May	1-15	0	0	0	4	0	0	0	5	0	5
	16-31	0	0	0	1	0	0	0	1	0	1
June	1-15	0	0	0	2	—	—	—	0	—	0
Total					131					192	174

^a One specimen showing molt in two or three areas.

^b Two specimens showing molt in two areas.

pattern unknown for any parulid (K. C. Parkes, in litt.) but found in two captive, hand-reared redstarts by E. Morton (see Rohwer et al. 1980). We eliminated the first of these possibilities because the prebasic molt occurs on the breeding ground (Petrides 1943) and a direct molt into the definitive plumage by some young males would likely have been discovered either by the collection of molting specimens exhibiting such a transition in appearance or by the discovery of autumn males in full breeding color but without fully ossified skulls. The second possibility, of a complete prealter-nate molt, could only be evaluated by a study of the reputed prealter-nate molt.

METHODS

Our results are based exclusively upon the examination of museum specimens. Over 500 specimens from the wintering grounds and over 50 spring and autumn specimens from the eastern United States were examined for molt. The minimum numbers of specimens upon which we have based our conclusions can be deduced from the totals in Tables 1 and 2 and Fig. 1.

All specimens of subadult males that were from the wintering grounds or were presumed to be in migration were checked for evidence of remige or retrix molt. For all specimens molt on the body was scored in five regions: throat—the anterior undivided portion of the ventral tract; breast—the middle portion of the ventral tract immediately posterior to its bifurcation; sides—the dorsal edges of the posterolateral branches of the ventral tract; head—the capital tract covering the crown of the head; and, back—the anterior portion of the dorsal tract. Using a dissecting microscope, we additionally checked male, but not female, specimens for molt of the rectal bristles and for molt around the eyes and in the lores. Most feathers in all of these body regions were lifted with a dissecting needle to check for small pin feathers or partially ensheathed feathers. To describe body molt quantitatively we used scores of: 0 = no molt, 1 = one or two growing feathers, 2 = three or four growing feathers, and so on to 5 = nine or more growing feathers.

For subadult males we quantified the amount of black feathering on the head, throat, back, and breast by measuring the area (mm^2) covered by black feathers in each of these regions. These measurements were made using a gridded sheet of acetate.

Operational definitions for categorizing specimens into the sex and age classes were: adult males—all birds in the definitive breeding plumage, regardless of the sex indicated on the label; females—only birds sexed as female and completely lacking black feathering; subadult males—all birds showing any black feathering that were not obviously adults and all birds sexed as male but with no black feathering.

Operational definitions for the geographic categorizations of specimens were: breeding grounds—any bird collected from the eastern United States north of the area along the gulf coast in which redstarts do not breed (see Peterson and Peterson 1980); migrants—specimens collected either in Florida or eastern Texas or right along the gulf coast south of the breeding range; wintering grounds—specimens from Mexico, Central and South America, and the West Indies. Obviously some specimens collected on the wintering and breeding grounds were migrating but we made no effort to classify such individuals separately.

To be included in Fig. 1 subadult males from the breeding grounds had to be collected between 1 September and 31 May. These criteria assured that all of the autumn specimens we included were hatched the preceding summer and that all of the spring specimens we included were approximately 1 year old.

RESULTS

If a molt is defined as having either a seasonal or a topographic regularity, then the black feathers that young male redstarts possess on their crown, back, throat, and breast seem not to be acquired in a molt but, rather, to be grown as a consequence of adventitious feather loss. This scattering of black feathers begins to appear in the autumn and slowly increases in number throughout the winter (Fig. 1). The seasonal distribution of specimens showing active molt of body feathers, exclusive of the rectal bristles or the feathers around the eyes or in the lores, suggests the

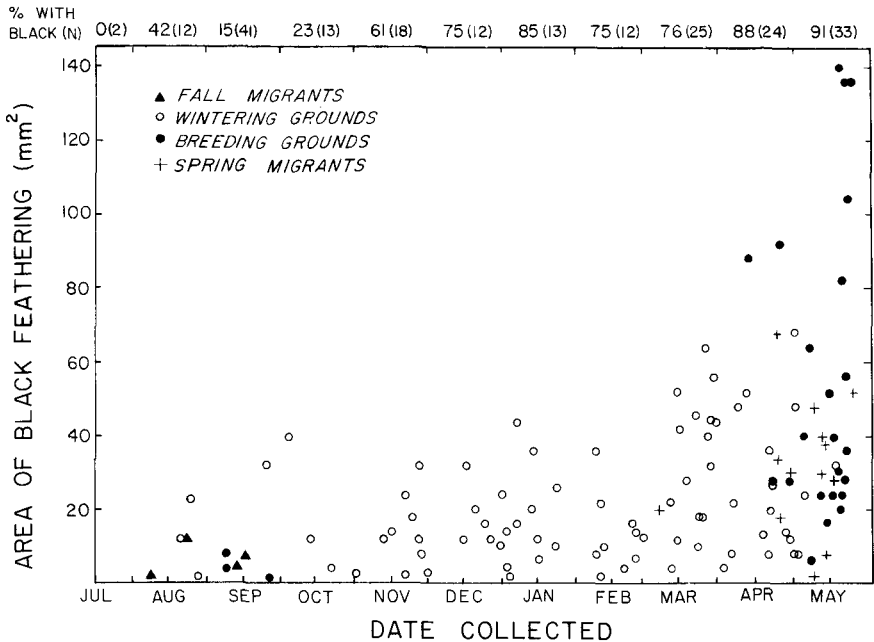


FIG. 1. Seasonal development of black contour feathers in yearling male American Redstarts. Individuals without black feathering are not plotted but are indicated by the sample sizes and frequencies across the top of the figure. One specimen from the wintering grounds taken on 19 December and having 184 mm² of black feathering was not plotted but is included in the frequency calculations across the top of this figure.

same conclusion: active feather replacement on specimens from the wintering grounds is rare and occurs from September through April (Table 1). The emergent vane of every partially ensheathed contour feather found on any subadult male examined from the wintering ground was black if it was growing in an area in which adult males are black.

Because of its topographic restriction, the at least partial replacement of the rictal bristles and of feathers around the eyes and in the lores might be considered a limited molt. Replacement of these feathers is somewhat (but not significantly) more intense in subadult than adult males when intensity is measured as proportion of specimens in active molt (19 of 131 vs 15 of 192 wintering specimens; $\chi^2 = 2.97$, $df = 1$, $P < 0.10$). Interestingly, the initiation of this protracted and very limited molt may be delayed in subadult males by about 2 months (Table 1).

The suggestion by Rohwer et al. (1980) that some young male redstarts acquire their definitive plumage in their first winter fails. No specimen

TABLE 2
FREQUENCIES OF YEARLING MALE AMERICAN REDSTARTS THAT SHOW BLACK FEATHERING
TABULATED IN SEASONAL AND GEOGRAPHIC CATEGORIES

Category	Number with black	Total	Percent
Autumn: breeding grounds	3	26	12
Autumn: migrants from gulf states	4	12	33
Wintering grounds: Aug. 1–Dec. 31	27	61	44
Wintering grounds: Jan. 1–June 1	54	70	77
Spring: migrants from gulf states	13	13	100
Spring: breeding grounds	23	24	96
Total	123	205	—

from the wintering ground was found to be in heavy molt. The highest molt score for all such specimens, including adult males and females, was that of a subadult male taken in December with a score of 12 out of a possible total of 25 (it had feathers growing on the head = 5, chin = 5, and sides = 2). A few subadults had one or more remiges or rectrices with the black and orange coloration characteristic of adults but the distribution of these feathers was always asymmetrical, indicating adventitious feather loss.

On the basis of two subadult males from New York that were growing black feathers in May, Dwight (1900) suggested that the “prenuptial molt” of yearling male American Redstarts took place rather late. Although we have not examined specimens from the breeding grounds for active molt, two points of our data suggest that some additional feather replacement occurs in subadult males as they are moving northward through the continental United States. First, and most importantly, the average amount of black feathering is considerably higher in subadults from the breeding grounds than in subadults taken in late winter or in spring migration (Fig. 1). Second, all but one of the 24 specimens from the breeding grounds that were categorized as a subadult male had scattered black feathering (Table 2). Undoubtedly this frequency change is partly a consequence of more reliable sexing of spring birds but we doubt that more reliable sexing is the entire explanation.

DISCUSSION

This study was undertaken to address two theoretically important questions. First, are young male American Redstarts bimodal in the timing of plumage maturation? Our failure to find evidence of a complete molt in over 130 winter-taken subadult males refutes this possibility. Second, is

the delayed plumage maturation of young male redstarts an adaptation to their first winter season or to their first potential breeding season?

If female-like, rather than adult-male-like, feathers were grown in a late winter prenuptial molt, then the subadult plumage worn by young male redstarts in their first potential breeding season could be inferred to be an adaptation to this first breeding season. Dwight (1900:288) reports that young male redstarts have a limited prenuptial molt and that "new white feathers on the chin are the rule." Contrary to this statement by Dwight (1900), our examination of specimens for active molt revealed no evidence that male redstarts ever grow female-like feathers after their first autumn. Thus, the molt pattern of American Redstarts fails to confirm either of the summer adaptation hypotheses (the CH or the FMH); although these data cannot reject these hypotheses they do make any explanation of subadult plumages invoking breeding adaptations less credible. Neither a winter nor a summer adaptive explanation of subadult plumages predicted our finding that young male redstarts are physiologically capable of producing black feathers soon after completion of the prebasic molt. Our data do not exclude the possibility that female-like feathers are grown in spring migration after subadults have reached the United States, but this seems most unlikely since some young males have acquired black feathers by August. Such specimens suggest that young males are physiologically "set" to produce black feathers soon after the completion of the prebasic molt.

For three unsatisfyingly weak reasons the subadult plumage of young male American Redstarts can more plausibly be considered an adaptation to their first winter than to their first potential breeding season. First, the absence of an extensive late winter molt in redstarts eliminates a physiological stress that in some species may help force subadults to migrate later in spring than adults. For example, both Purple Martins (*Progne subis*) and Indigo Buntings (*Passerina cyanea*) have a partial or extensive late winter molt and in both of these species subadult males return later than adults (Niles 1972, Rohwer and Niles 1979, Carey and Nolan 1979). The absence of an extensive late winter molt in redstarts renders more plausible the argument that the female-like plumage of subadult male redstarts in spring may be a cause, rather than a result, of their late spring arrival (Procter-Gray and Holmes 1981). Second, those feathers around the eyes and in the lores that do seem to be molted in late winter always come in black which is their color in adult males. Third, an explanation of the subadult plumage in redstarts invoking a wintering adaptation is consistent with the fact that winter but not summer subadult plumages occur in the young males of at least some other warblers in which a sexual dichromatism is maintained by adults in winter (e.g., Yellow Warbler [*Dendroica petechia*], Mourning Warbler [*Oporornis philadelphia*], and

Canada Warbler [*Wilsonia canadensis*]). Although this last observation suggests that winter has to be the season to which most immature plumages of male warblers are adapted, it demands an explanation of the absence of a prenuptial molt that would bring young male American Redstarts and Olive Warblers into the definitive plumage for their first breeding season.

We know of only two other studies of the winter molt of species in which males have a subadult plumage in their first potential breeding season, that of Niles (1972) for Purple Martins and Parkes (1967) for eastern Summer Tanagers (*Pyrranga rubra rubra*). Nothing can be concluded from these studies regarding winter vs summer explanations of subadult plumages because the color of incoming feathers on specimens in active molt was not indicated. The mottled appearance of subadult male Summer Tanagers of the eastern race (*rubra*) and of subadult male Purple Martins proves that they do grow feathers of the definitive plumage in their first winter. While this observation supports the WAH, the evidence is inconclusive for two reasons. First, the possibility that young males also grow female-like feathers in this winter molt has not been excluded for either species; and second, most male Summer Tanagers of the western race (*cooperi*) are entirely female-like in their first potential breeding season (Rohwer et al. 1980). In summary, no general conclusion concerning the season to which subadult male breeding season plumages are adapted can yet be suggested from interspecific comparisons of molt patterns. Such a comparative study must await quantitative molt studies in those species having both a late winter molt and featuring delayed plumage maturation of males in their first potential breeding season (e.g., various orioles [*Icterus* spp.], cardinal grosbeaks [*Passerina* spp., *Pheucticus* spp.], and tanagers [*Piranga* spp.]).

Why should the prealternate molt of young male redstarts be limited to the rictal bristles and to the feathers around the eyes and in the lores? A possible explanation is related to foraging needs. The importance of rictal bristles in protecting the eyes of an aerial forager was recently confirmed by Conover and Miller (1980). Many birds have black lores or black feather patches around their eyes. Possibly the function of black color around the eye and, especially of the smooth upper mandible is to reduce glare, thus increasing visual acuity (Burt 1981). Recently E. H. Burt (pers. comm.) has confirmed the possible detrimental effect of glare on prey capture in Willow Flycatchers (*Empidonax traillii*). Individuals with their upper bill painted white foraged more often in the shade than did controls, arguably because their ability to target prey in full sun had been reduced by the experimentally increased glare (Burt, unpubl.). Given that young male redstarts are physiologically capable of growing black feathers, a limited molt producing black feathers around the eyes may improve the prey cap-

ture rate of young males for their first potential breeding season. Such an explanation presumes that females and first winter males which lack this black feathering forage more in the shade than do adult males; data related to these sex and age differences in foraging ecology do not seem to be available.

SUMMARY

Two seasonal classes of hypotheses may be invoked to explain the delayed plumage maturation of males in sexually dichromatic passerine species. The female-like plumage of first-year males could be an adaptation either to their first potential breeding season or to their first winter. Proof that the female-like feathering is an adaptation to the first potential breeding season would be provided by showing that female-like, rather than adult-male-like, feathers were grown in a late winter molt. This molt could either be a delayed prebasic (i.e., post juvenile) molt as in Purple Martins (*Progne subis*) or a prealternate molt as occurs in tanagers.

Contra Dwight (1900) no female-like feathers are grown by subadult male American Redstarts (*Setophaga ruticilla*) in a prealternate molt. Both adult and subadult male redstarts have a very limited prealternate molt involving at least some of the rictal bristles and the feathers around the eyes and in the lores. This molt seems related to increasing foraging efficiency. Contrary to the suggestion by Rohwer et al. (1980), young male redstarts are not polymorphic in the age at which they achieve plumage maturity: young males probably never achieve the definitive plumage in their first prebasic molt and none of over 130 winter-taken first-year males showed evidence of an extensive or a complete prealternate molt. Our data for young male redstarts are more consistent with winter than summer being the season to which their subadult plumage is adapted; however, this conclusion is weak because of the very limited late winter feather replacement in redstarts.

ACKNOWLEDGMENTS

Specimens for this work were kindly made available by curators at the following institutions: American Museum of Natural History, California Academy of Sciences, Carnegie Museum, Delaware Museum of Natural History, Field Museum of Natural History, Florida State Museum, Los Angeles County Museum, Louisiana State University, Museum of Comparative Zoology, Philadelphia Academy of Natural Sciences, Tall Timbers Research Station, University of Michigan, University of Washington, U.S. National Museum, and Yale Peabody Museum of Natural History. We are grateful to K. Parkes for his inexhaustible commentary on the project and to D. Holmes, G. Butcher, F. Rohwer, M. Foster, and J. Burt, for helpful comments on the manuscript. This work was partly supported by NSF grant BNS 80-08957.

LITERATURE CITED

- BURTT, E. H., JR. 1981. The adaptiveness of animal colors. *Bioscience* 31:723-729.
- CAREY, M. AND V. NOLAN, JR. 1979. Population dynamics of Indigo Buntings and the evolution of avian polygyny. *Evolution* 33:1180-1192.
- CONOVER, M. R. AND D. E. MILLER. 1980. Rictal bristle function in Willow Flycatcher. *Condor* 82:469-471.
- DWIGHT, JONATHAN, JR. 1900. The sequence of plumage and moults of the passerine birds of New York. *Annals N.Y. Acad. Sci.*, 13:73-360.
- NILES, D. M. 1972. Molt cycles of Purple Martins (*Progne subis*). *Condor* 74:61-71.
- PARKES, K. C. 1967. Prealternate molt in the Summer Tanager. *Wilson Bull.* 79:456-458.

- PETERSON, R. T. AND V. M. PETERSON. 1980. A field guide to the birds. Houghton Mifflin Co., Boston, Massachusetts.
- PETRIDES, G. A. 1943. Notes on a captive redstart. *Wilson Bull.* 55:193-194.
- PROCTER-GRAY, E. AND R. T. HOLMES. 1981. Adaptive significance of delayed attainment of plumage in male American Redstarts: tests of two hypotheses. *Evolution* 35:742-751.
- ROHWER, S. 1983. Testing the female mimicry hypothesis of delayed plumage maturation: a comment on Procter-Gray and Holmes. *Evolution* 37:421-423.
- , S. D. FRETWELL, AND D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am. Nat.* 115:400-437.
- AND D. M. NILES. 1979. The subadult plumage of male Purple Martins: variability, female mimicry and recent evolution. *Z. Tierpsychol.* 51:282-300.
- SELANDER, R. K. 1965. On mating systems and sexual selection. *Am. Nat.* 99:129-141.
- WEBSTER, J. D. 1958. Systematic notes on the Olive Warbler. *Auk* 75:469-473.

DEPT. ZOOLOGY NJ-15 AND WASHINGTON STATE MUSEUM DB-10, UNIV.
WASHINGTON, SEATTLE, WASHINGTON 98195. ACCEPTED 21 DEC. 1982.