Molt-migration in the American Redstart (*Setophaga ruticilla*) revisited: Explaining variation in feather δD signatures.—At least once a year, birds face the energetically demanding task of molting all their flight and body feathers. As a result, most birds avoid an overlap between molt and other costly activities during the annual cycle (e.g., raising young, migrating). Most Nearctic–Neotropical migratory birds undergo an entire prebasic molt at the end of the breeding season, before fall migration, and some also go through a second, pre-alternate molt of body feathers on the wintering grounds to refurbish their breeding plumage

before reproduction (Pyle 1997, Froehlich et al. 2005). Even so, some birds employ a strategy of molt-migration, delaying some or all of their prebasic molt until after fall migration begins (Stresemann and Stresemann 1966). This phenomenon is relatively common in shorebirds, and nearly half the Neotropical migrants molt at least some feathers south of the breeding grounds (Leu and Thompson 2002). However, molt-migration is not nearly as frequent in passerines (e.g., only 7 of 53 wood warblers are reported to complete at least some of their prebasic molt outside of the breeding grounds: *Vermivora peregrina*, *V. celata*, *V. luciae*, *Dendroica petechia*, *D. pensylvanica*, *D. kirtlandii*, and *Protonotaria citrea*; Pyle 1997), and it also appears to vary geographically, occurring more commonly in western North America (Rohwer et al. 2005).

In a recent study, Norris et al. (2004b) suggested that molt-migration is a conditional strategy in American Redstarts (*Setophaga ruticilla*) whereby individuals investing in late-season parental effort (i.e., birds fledging more young late in the breeding season) delay part of their molt until sometime during migration. Using stable-hydrogen isotopes (δD) in tail feathers to infer the latitude of molt, Norris et al. (2004b) showed that reproductive effort was positively correlated with δD values the following year. Additionally, birds that fledged young had tail feathers with more positive δD values (indicative of molt at a southerly stopover site) than individuals that did not fledge offspring. Birds presumed to be molt-migrants also had less red plumage (lower red chroma values), which suggests a tradeoff between current and future reproduction, if plumage is an important sexual signal.

Since the publication of Norris et al.'s (2004b) paper, studies examining isotopic variation have determined that δD is more variable within populations than was previously assumed (Wunder et al. 2005, Powell and Hobson 2006, Rocque et al. 2006, Langin et al. 2007). For example, in the same American Redstart population studied by Norris et al. (2004b), Langin et al. (2007) reported 22‰ variation in δD (first primary [P1], range: –92 to –70‰, mean = –82 ± 4‰ SD, $n = 42$) among feathers grown by different individual birds that bred within 2 km of each other during the year of molt, suggesting that some birds Norris et al. (2004b) presumed to be molt-migrants may have grown their tail feathers locally using hydrogen sources with more positive δD values than expected (Norris et al. [2004b] estimated a range of –88 to –72‰).

In the present study, we report additional data on the relationship between reproductive effort, molt location (as inferred by δD analysis), and feather color to test the robustness of these relationships and to further document the frequency of molt-migration. We also test an alternative hypothesis that a high degree of variation of δD on the breeding grounds, coupled with inadvertent feather loss during the non-breeding period, can explain the occurrence of individuals returning to the breeding grounds with more positive δD signatures and tail feathers with lower red chroma.

Methods

Breeding population.—Work on the breeding grounds was conducted May–July, 2004–2007, at the Queen's University Biological Station, Chaffey's Lock, Ontario (44°34′N, 76°19′W), using the same study population of American Redstarts as Norris et al. (2004b) and Langin et al. (2007). All birds were captured and processed following Norris et al. (2004b). One difference, however, is that none of our nests was experimentally depredated as was done with a subset of birds by Norris et al. (2004b; see Langin et al. 2006). We also collected the first primary (P1) from all individuals and a second rectrix from individuals with regrown tail feathers (i.e., feathers that appeared less orange than the rest of the feathers, were unworn and had narrow growth bars).

Overwintering population.—American Redstarts were also studied at a wintering site consisting of high-quality (dominated by Black Mangrove [*Avicennia germinans*]) and low-quality (second-growth scrub dominated by Logwood trees [*Haematoxylon campechianum*]) habitats from January to March, 2004 and 2005, at Font Hill Nature Preserve, Westmoreland Parish, Jamaica (18°02′N, 77°57′W; see Marra 2000). We studied birds overwintering in Jamaica because populations breeding in the northeastern United States and southern Ontario appear to overwinter in the Caribbean (Norris et al. 2006), which suggests that conditions in Jamaica should be similar to those experienced by our breeding population during the non-breeding season.

We tested the hypothesis that birds previously reported as molt-migrants may have lost and subsequently regrown tail feathers on the wintering grounds and that feather regrowth may be condition-dependent. To do this, we captured birds in Jamaica during January–February, weighed them to the nearest 0.1 g, and plucked a single tail feather (R3). Before spring departure, we recaptured the same individuals to determine overwinter change in body mass and whether they regrew the plucked feather. Feathers were defined as "regrown" if they extended >1 cm from the feather sheath. For a subset of birds ($n = 10$ ASY males), we then plucked the regrown feather for comparisons of δD and color between the original and regrown feathers.

Stable-hydrogen-isotope and color analyses.—Details of our stable-hydrogen-isotope analysis are reported in Langin et al. (2007) and are the same as those employed by Norris et al. (2004b). Reflectance spectra from tail feathers were obtained by measuring percent reflectance from 320–700 nm using an Ocean Optics USB2000 spectrometer attached to a PX-2 xenon pulsed light source. The sheathed probe was held at a 90° angle to the feather surface. All feathers were mounted on minimally reflective (<5% reflectance) black paper (Colorline no. 142 Ebony). To standardize our measurements, we took dark and white (spectralon) standard readings between each measurement and the next. Twenty-five measurements were taken haphazardly within the yellow–orange region of each tail feather, avoiding the rachis. We then averaged across the 25 reflectance spectra and quantified plumage coloration by calculating standard measures of brightness, hue, and chroma (Montgomerie 2006). Our measure of red chroma is the same as that reported by Norris et al. (2004b): brightness = mean $R_{320-700}$, hue = $\arctan([(R_{415-510} - R_{320-415})/R_{320-700}]/[(R_{575-700} - R_{415-575})/R_{320-700}])$, UV chroma = $R_{320-415}/R_{320-700}$, and red chroma = $R_{575-700}/R_{320-700}$.

Data analysis.—Following Norris et al. (2004b), reproductive effort was calculated as a combination of the number of young fledged and fledging date, where birds with reproductive-effort scores of 0 did not fledge offspring and birds with the highest reproductive-effort scores fledged more offspring later in the season. All statistical analyses were performed in JMP 7.0 (SAS Institute 2007).

Results

Isotopic signatures.—Adult males known to have bred at our study site in 2004 and 2005 returned the next year with tail feather δD values that ranged from −92 to −64‰ ($n = 26$), with an average value of −78 ± 7‰ SD. Two of these males had δD values that fell just outside the previously reported range of variation at our study site (−92 to −70‰; Langin et al. 2007), with δD values of −64‰ and −69‰. We found no difference in δD between the first primary (P1), which should always be molted first on the breeding grounds (Pyle 1997), and tail feathers (R3; $t_{15} = -1.59$, $P = 0.13$).

Reproductive effort.—There was no relationship between reproductive effort in year x and δD the following year ($r^2 = 0.02$, $P = 0.58$, $n = 16$), no difference in δD between birds that did and did not fledge offspring the previous season ($t_{14} = -0.71$, $P = 0.49$; 7 no, 9 yes), and no relationship between fledging date in year x and δD the following year ($r^2 = 0.22$, $P = 0.29$, $n = 7$). We also found no relationship between reproductive effort in year x and red chroma ($r^2 = 0.0005$, $P = 0.91$, $n = 26$), UV chroma ($r^2 = 0.001$, $P = 0.86$, $n = 26$), hue ($r^2 = 0.0006$, $P = 0.90$, $n = 26$), or brightness ($r^2 = 0.08$, $P = 0.16$, $n = 26$). Finally, there was no relationship between δD and red chroma ($r^2 = 0.02$, $P = 0.38$, $n = 50$), UV chroma ($r^2 = 0.06$, $P = 0.08$, $n = 50$), hue ($r^2 = 0.05$, $P = 0.14$, $n = 50$), or brightness ($r^2 = 0.03$, $P = 0.23$, $n = 50$).

Feather regrowth.—From 2005 to 2007, 7% (4 of 56) of adult males captured at our study site in Ontario had one or more tail feathers that were clearly regrown, which also had more positive δD values (−42, −48, −49, and −54‰) in relation to mean δD value of locally grown adult flight feathers (−82 ± 4‰; Langin et al. 2007). In the feather regrowth experiment on the wintering grounds, the δD of the original feather plucked from adult males averaged −73 ± 3‰ ($n = 10$). By contrast, δD of regrown feathers from the same individuals plucked when recaptured later in winter averaged −35 ± 2‰ ($n = 10$; $t_8 = 11.68$, $P < 0.0001$; Fig. 1A). Those same feathers had significantly lower red chroma values ($t_8 = -3.70$, $P = 0.005$; Fig. 1B) and hue ($t_8 = -6.61$, $P < 0.0001$), but not UV chroma ($t_8 = 1.13$, $P = 0.29$) or brightness ($t_8 = 0.61$, $P = 0.56$).

The probability of regrowing an experimentally plucked tail feather during the non-breeding season in Jamaica was higher among American Redstarts that maintained or gained mass between captures (Wald's $\chi^2 = 6.42$, $P = 0.01$). Variation among birds in the time elapsed between capture and recapture did not influence the probability of feather replacement (Wald's $\chi^2 = 0.00$, $P = 0.98$).

Discussion

Over the two years of the present study, we found no substantive evidence of molt-migration in American Redstarts and no support for a reproductive tradeoff. Only 2 of 26 return breeders had feathers with δD values (−64 and −69‰) that were marginally outside the known range of variation at our study site (i.e., values greater than −70 ‰; Langin et al. 2007). Furthermore, no American Redstarts that returned to breed had tails with highly positive δD signatures and low red chroma.

Unlike the previous study by Norris et al. (2004b), which suggested that molt-migration could be driven by reproductive effort, we found no difference in δD between males that did and did not fledge offspring the previous season and no relationship between
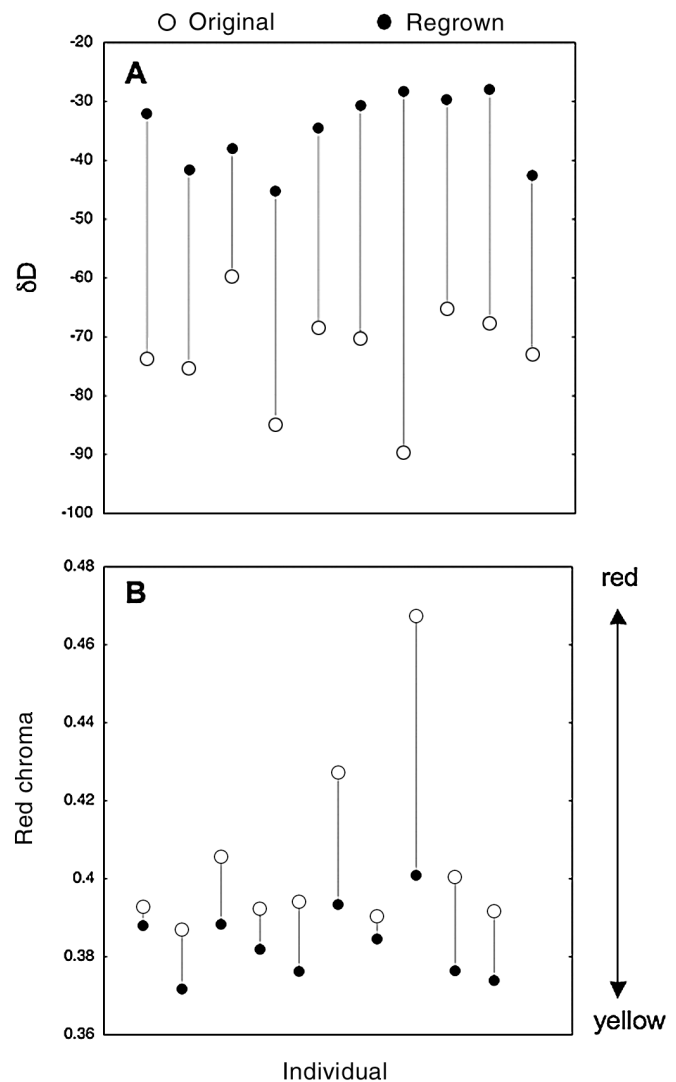

Fig. 1. (A) δD signatures and (B) red chroma of original (open circles) and regrown (closed circles) feathers of adult males originally captured in January–February on the wintering grounds in Jamaica and subsequently recaptured before spring departure ($n = 10$).

reproductive effort and δD. One of the major implications of Norris et al.'s (2004b) study was that late-season parental effort could result in a tradeoff between current and future reproduction, given that birds with more positive δD signatures (presumed molt-migrants) also had feathers with lower red chroma values. We found no relationship between δD and red chroma and no relationship between reproductive effort in year x and red chroma the following breeding season.

Results from our feather regrowth experiment demonstrated, as expected, that feathers regrown in Jamaica have significantly more positive δD signatures and lower red chroma values (Fig. 1). This pattern is consistent with observations from our breeding population and from the Powdermill Avian Research Center (Rector, Pennsylvania), where a few individuals arrive with one or two yellow tail feathers that are clearly distinguishable from

the orange tail feathers (R. S. Mulvihill pers. comm., M. W. Reudink and K. M. Langin pers. obs.). During the present study, 7% of the birds had clearly regrown a tail feather (see above), which also had highly positive δD signatures, which is consistent with overwinter regrowth. We suggest that the pattern observed by Norris et al. (2004b) was more likely driven by adventitious molt during the overwintering period in a few individuals, resulting in feathers with highly positive δD signatures and low red chroma (consistent with the regrown feathers in our feather regrowth experiment).

Regardless of the mechanism that results in highly positive δD signatures and low red chroma, the fact that Norris et al. (2004b) detected a relationship between reproductive effort and δD–feather color is intriguing. One explanation for this result may be condition-dependent feather regrowth on the wintering grounds. In Jamaica, individuals that maintained or gained mass during winter were more likely to regrow feathers than individuals that were unable to maintain mass in winter. Previous research indicates that differences in mass-change during the overwintering period are driven by habitat quality (Marra and Holmes 2001, Studds and Marra 2005). Furthermore, birds in high-quality habitats have lower corticosterone levels (Marra and Holberton 1998), depart the wintering grounds earlier (Marra and Holberton 1998, Studds and Marra 2005), arrive on the breeding grounds earlier (Marra et al. 1998, Norris et al. 2004a, Reudink et al. unpubl. data), and ultimately fledge more offspring and have higher reproductive success (Norris et al. 2004a, Reudink et al. unpubl. data). Therefore, these birds would have been more likely to be classified as molt-migrants according to Norris et al. (2004b). We suggest that birds in good condition during winter are more likely to fledge offspring the following breeding season and are also more likely to have regrown any feathers lost during winter on the wintering grounds (as opposed to not regrowing lost feathers). On the other hand, birds that do not regrow lost feathers during the overwinter period are likely to have been in poor condition during winter and are less likely to fledge offspring. Thus, individuals arriving with adventitiously molted feathers are more likely to be high-quality birds that fledged offspring.

Finally, the results in the Norris et al. (2004b) study were driven primarily by three individuals with extremely high δD values and low red chroma. It is possible that the observed relationship with reproductive effort may be a spurious result driven by a small number of birds with adventitiously molted feathers that happened to fledge young late in the season.

Our inability to find evidence of molt-migration in our breeding population of American Redstarts, combined with the results of our feather regrowth experiment, suggest that molt-migration is unlikely to play a role in structuring American Redstart life history. Furthermore, our results are consistent with a lack of evidence of molt-migration at banding stations. In nearly five decades of capturing fall-migrating American Redstarts at both the Powdermill Avian Research Center and Long Point Bird Observatory (Long Point, Ontario), investigators have not detected a single molt-migrant among the thousands of American Redstarts captured (R. S. Mulvihill pers. comm., D. J. T. Hussell pers. comm.).

—Matthew W. Reudink, *Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada, and Smithsonian Migratory Bird Center, 3001 Connecticut Avenue NW, Washington, D.C. 20008, USA (E-mail: reudinkm@si.edu)*; Peter P. Marra, *Smithsonian Migratory Bird Center, 3001 Connecticut Avenue NW, Washington, D.C. 20008, USA*; Kathryn M. Langin, *Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada, and Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA*; Colin E. Studds, *Smithsonian Migratory Bird Center, 3001 Connecticut Avenue NW, Washington, D.C. 20008, USA, and Program in Behavior, Ecology, Evolution, and Systematics, University of Maryland, College Park, Maryland 20742, USA*; T. Kurt Kyser, *Department of Geological Sciences and Geological Engineering, Queen's University, Kingston, Ontario K7L 3N6, Canada*; and Laurene M. Ratcliffe, *Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada.*

Literature Cited

Froehlich, D. R., S. Rohwer, and B. J. Stutchbury. 2005. Spring molt constraints versus winter territoriality: Is conspicuous winter coloration maladaptive? Pages 321–335 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Langin, K. M., D. R. Norris, T. K. Kyser, P. P. Marra, and L. M. Ratcliffe. 2006. Capital versus income breeding in a migratory passerine bird: Evidence from stable-carbon isotopes. Canadian Journal of Zoology 84:947–953.

Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe. 2007. Hydrogen isotopic variation in migratory bird tissues of known origin: Implications for geographic assignment. Oecologia 152:449–457.

Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: A review for Neotropical migrants. Biological Conservation 106:45–56.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Marra, P. P., and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: Effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116:284–292.

Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. Auk 118:92–104.

Montgomerie, R. 2006. Analyzing colors. Pages 90–147 in Bird Coloration: Mechanisms and Measurements, vol. 1 (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.

Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed Neotropical–Nearctic songbird, the American Redstart (*Setophaga ruticilla*). Pages 14–28 in Patterns of Migratory Connectivity in two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004a. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London, Series B 271:59–64.

Norris, D. R., P. P. Marra, R. Montgomerie, T. K. Kyser, and L. M. Ratcliffe. 2004b. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306:2249–2250.

Powell, L. A., and K. A. Hobson. 2006. Enriched feather hydrogen isotope values for Wood Thrushes sampled in Georgia, USA, during the breeding season: Implications for quantifying dispersal. Canadian Journal of Zoology 84:1331–1338.

Pyle, P. 1997. Identification Guide to North American Birds, part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.

Rocque, D. A., M. Ben-David, R. P. Barry, and K. Winker. 2006. Assigning birds to wintering and breeding grounds using stable isotopes: Lessons from two feather generations among three intercontinental migrants. Journal of Ornithology 147:395–404.

Rohwer, S., L. K. Butler, and D. R. Froehlich. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 in Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

SAS Institute. 2006. JMP Statistical Discovery, version 6.0.2. Duxbury, Pacific Grove, California.

Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vogel. Journal für Ornithologie 107 (Suppplement):1–447.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. Oecologia 144:607–617.