Continent-wide variation in feather colour of a migratory songbird in relation to body condition and moultng locality

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Understanding the causes of variation in feather colour in free-living migratory birds has been challenging owing to our inability to track individuals during the moultng period when colours are acquired. Using stable-hydrogen isotopes to estimate moultng locality, we show that the carotenoid-based yellow–orange colour of American redstarts (Setophaga ruticilla) tail feathers sampled on the wintering grounds in Central America and the Caribbean is related to the availability of carotenoids. Hence, individuals that were moulted more orange–red feathers further north. Independent samples obtained on both the breeding and the wintering grounds showed that red chroma—an index of carotenoid content—was not related to the mean daily feather growth rate, suggesting that condition during moult did not influence feather colour. Thus, our results support the hypothesis that feather colour is influenced by ecological conditions at the locations where the birds moulted. We suggest that these colour signals may be influenced by geographical variation in diet related to the availability of carotenoids.

Keywords: migration; carotenoids; stable isotopes; feather growth

1. INTRODUCTION

Tissue colours, such as those on feathers, that are derived from ingested carotenoids are important signals of animal health and individual quality (Lozano 1994; Olson & Owens 1998). However, understanding the mechanisms that influence variation in feather colour in migratory birds has been challenging owing to the difficulty in tracking individuals during the moultng period when colour-producing carotenoids are incorporated into growing feathers. In this study, we use a novel approach to examine the causes of variation in feather colour in the American redstart (Setophaga ruticilla), a small (8 g) migratory songbird that breeds in North America and winters in the Caribbean and Central America. Conspicuous patches on their tail and flight feathers vary in colour from yellow to red–orange (Norris et al. 2004) and are produced from carotenoids acquired from their insectivorous diet (McGraw 2006). Redstarts conduct a complete moult once a year soon after breeding, typically just before fall migration (Sherry & Holmes 1997).

Recently, we showed that redstarts moulting at a breeding site in Ontario, Canada produced tail feathers that had higher red chroma values (a measure of colour saturation reflecting the type or concentration of carotenoids; Saks et al. 2003) than individuals breeding at the same site but moulted at more southerly locations during autumn migration (Norris et al. 2004). Here, we explore two hypotheses to explain this pattern. First, the ‘condition hypothesis’ proposes that dull-coloured tissues are produced because individuals are in relatively poor physiological condition (Hill & Montgomerie 1994). Since carotenoids have important roles in endocrine and immune systems, the prediction is that individuals in poor body condition should have fewer carotenoids available for tissue coloration (Olson & Owens 1998). To assess this hypothesis, we examined feather colour (red chroma) in relation to the daily growth rate of feathers from both a breeding site in Ontario and across the tropical wintering range. Feathers sampled in both of these periods were grown at the end of the previous summer, and thus indicate both colour and condition during moult. Second, the ‘environmental constraints hypothesis’ proposes that variation in feather colour arises primarily from differences in the type or the concentration of carotenoids consumed, which may vary geographically (Hill et al. 1994; McGraw 2006). To assess this hypothesis, we examined the relationship between red chroma and moulting latitude (estimated by stable-hydrogen isotopes (δD)) of tail feathers sampled throughout the wintering range. δD is incorporated into animal tissue from the local diet and can be used as a geographical tracer of the moulting locality because it reflects the latitudinal variation in δD from precipitation (Hobson & Wassenaar 1997).

2. MATERIAL AND METHODS

(a) Feather sampling

On the breeding grounds (May–June 2001–2004), we sampled tail feathers from male redstarts captured at the Queen’s University Biological Station (44°34’N, 76°19’W) in southeastern Ontario, Canada. Individuals marked in year x were recaptured in year x+1 and a single tail feather (third retrix) was removed (Norris et al. 2004), thus providing an estimate of feather growth rate during the annual moult in year x. We also sampled a third retrix from after-hatch-year (AHY; second wintering season or older) and hatch-year (HY; first wintering season) males (n=122) at 12 locations throughout the wintering range (9.3°–32.2°N and 60.6°–105.7°W; figure 1a). We collected feathers in January–March 2001–2004, except from the Dominican Republic (1997) and Belize (1999).

(b) Analysis of moulting region

We used stable-hydrogen isotopes (δD) to estimate moultng location. Stable-hydrogen isotope ratios (H/H = δD) are expressed in δ notation (‰) where δ = [(Rsample/Rstandard) − 1] × 1000 and Rstandard is the hydrogen isotope ratio of Vienna Standard Mean Ocean Water. For a detailed description of sample preparation and analysis, see Norris et al. (2006). δD values in feathers sampled on the wintering grounds (January–March) indicate moulting latitude the previous July–September. Norris et al. (2006) used a likelihood assignment method to estimate the moulting regions (figure 1a) of individuals that were sampled on the wintering grounds, based on

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expected $\delta D$ values in precipitation and relative breeding abundance. We found no significant variation in $\delta D$ values among years within localities (Norris et al. 2006), hence we pooled samples across years for each locality.

(c) **Feather colour analysis**
We measured reflectance across the bird-visible spectrum (320–700 nm) of five haphazardly chosen areas within each yellow-orange colour patch on each tail feather using an Ocean Optics USB2000 spectrometer connected to a PX-2 pulsed xenon light source (Norris et al. 2004). From each spectrum, we calculated red chroma as the proportion of total reflectance from the orange-red region of the spectrum (575–700 nm) and calculated the mean for each individual. Red chroma is a measure of spectral purity in that part of the spectrum (Montgomerie 2006) and is correlated with the amount of carotenoids deposited in the feather (Saks et al. 2003).

Biol. Lett.
3. RESULTS AND DISCUSSION

For feathers sampled on the breeding grounds, mean daily feather growth rate of AHY males was not significantly related to δD-values ($r^2 = 0.17, p = 0.47, n = 23$). Moreover, based on expected δD values of AHY males breeding in Ontario (Norris et al. 2004), we found no significant difference in mean feather growth rates of birds that moulted on the breeding grounds versus those that moulted further south during migration (one-tailed t-test, $t_{21} = -0.79, p = 0.22$).

Similarly, for AHY males sampled on the wintering grounds, there was no relationship between feather growth rate and δD values for HY males ($r = -0.30, p = 0.04, n = 47$), suggesting that nestlings at higher latitudes grew feathers faster. Nonetheless, red chroma was not significantly related to the growth rate of feathers sampled on either the breeding ($r = 0.22, p = 0.33, n = 23$) or the wintering grounds (ANCOVA, $R^2 = 0.14$, no significant interactions; growth rate effect, $F_{1,104} = 0.30, p = 0.58$; δD effect, $F_{1,104} = 6.69, p = 0.01$; age effect, $F_{1,104} = 10.7, p = 0.001$; figure 1b), suggesting that condition during moult did not influence carotenoid concentration of the feathers. We included mouling latitude as a factor in this analysis to control for local environmental effects that could confound the relationship between feather growth rate and colour.

Next, we examined whether feather colour was related to large-scale geographical differences in mouling location (figure 1a). Previously, we reported a significant negative correlation between red chroma and δD-values in feathers sampled on the breeding grounds (Norris et al. 2004). For males sampled throughout the wintering range, there was a similar negative relationship between red chroma and δD-values (ANCOVA, $R^2 = 0.14$, no significant interactions; δD effect, $F_{1,102} = 6.7, p = 0.01$, standardized $\beta = -0.24$; age effect, $F_{1,102} = 10.7, p = 0.002$; figure 1c), providing additional evidence that moult ing location influences feather colour. Similarly, red chroma varied significantly among regions (one-way ANOVA, $F = 2.22$, no interaction term; mouling region effect, $F_{8,99} = 4.2, p = 0.003$; figure 1d), with males moult ing in the southeast (SE) region having significantly lower red chroma than two (MW and NE) of the three northern regions ($p < 0.05$; Tukey’s post hoc tests).

Our results thus support the idea that feather colour is influenced by geographical variation in mouling location. We provide independent evidence, from males sampled thousands of kilometres apart in different periods of the annual cycle (winter and summer), that feathers with low red chroma were most likely grown at low latitudes in the southeastern US. We suggest two possible reasons for this pattern. First, redstarts moulting at lower latitudes may consume insects with lower carotenoid concentrations. There are no data available to test this idea, and to the best of our knowledge there is no information on geographical variation in carotenoids in avian diets. Anecdotal evidence suggests that redstarts may consume small amounts of carotenoid-rich fruits during moult (Sherry & Holmes 1997), which could also vary geographically. Second, the absorption, conversion or acquisition of carotenoids may be influenced by parasite loads (Brawner et al. 2000) and, if the incidence and virulence of avian parasites vary among populations of migratory birds (Piersma 1997), then this could also influence geographical variation in colour. If parasites influence colour in redstarts, however, we would have expected to see a relationship between red chroma and feather growth rate, since birds with high parasite loads should also be in relatively poor condition (Hill & Montgomerie 1994).

Since our results suggest that geographical variation in feather colour may arise through ecological differences between regions, the colonization of new areas could lead to differences in the colour of carotenoid-based tissues. If changes in male colour result in a modification or adjustment in female choice, then reproductive isolation could also be influenced by environmentally induced phenotypic traits (e.g. Boughman 2001). We suggest future studies to examine the patterns and mechanisms of geographical variation in dietary carotenoids to help address this interesting question.

We demonstrate here how the combination of novel analytical techniques applied to a single feather can reveal unique insights into avian ecology. Many migratory birds are difficult to track during the secretive moult ing period, hence the use of stable isotopes provides a method to estimate their moult ing locality no matter where or when they are sampled. When combined with advanced colour measurement techniques (Andersson & Prager 2006), our approach can be used to rapidly assess relationships between moult ing latitude and feather colour in a variety of species with different life-history strategies and geographical ranges.

Supported by grants from Smithsonian Institution Scholarly Studies program (P.P.M. and D.R.N.), NSF (0085965, P.P.M.), NSERC (R.M., T.K.K., L.M.R. and D.R.N.) and the Canadian Foundation for Innovation (T.K.K.).
to K. Langin, M. Reudink, B. Fedy, K. Klassen, A. Vuletich, C. Cliffe and J. Clarke for field and laboratory assistance.


