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Delayed maturation of multiple signals in a migratory songbird

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Abstract Many animals use multiple signals in sexual communication, but our understanding of the interactions between multiple signals, particularly in inexperienced breeders, is limited. In birds, delayed plumage maturation (DPM) is well documented; young birds appear duller than adults, despite reaching sexual maturity. Age-related changes in song structure are also common in songbirds, though the extent to which songs of yearling males differ from those of adults (delayed song maturation, DSM) and its prevalence in species with DPM is unknown. We tested for DSM in the mate-attraction (repeat) song of a species with dramatic DPM, the American redstart (*Setophaga ruticilla*). Repeat song structure of territorial yearling and adult males differed significantly, based on discriminant

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analysis of nine non-collinear song features. Combined with previous evidence of delayed maturation in territorial (serial) song, we provide the first evidence for DSM in different song types used in different behavioral contexts during the breeding season of a migratory songbird. Within adults, variation in repeat song was associated with pairing, earlier onset of breeding, and number of offspring sired, suggesting a potential benefit for expressing more adult-like song. We found no relationship between the expression of adult-like repeat song and plumage in either age class. These results indicate that delayed maturation of repeat song in yearling redstarts is not due to a generalized delay in signal development, and suggest further work is needed to determine whether mate attraction (for both yearling and adult males) provides greater pressure to sound more "adult-like" than to look more "adult-like".

Keywords Delayed song maturation \cdot Delayed plumage maturation \cdot Multiple signals \cdot Mate choice \cdot American redstart

Introduction

Many animals display and perceive more than one signaling trait in sexual communication. Because animals communicate using multiple sensory systems, careful consideration of multiple aspects of sensory emission is necessary to understand the role of sexual signals (Partan and Marler 2005). Several hypotheses attempt to explain the evolution of multiple signals, including the "redundant signal" (multiple ornaments signal overall individual quality), "multiple message" (different ornaments signal different properties), and "unreliable signal" (uncorrelated signals become exaggerated by runaway selection) hypotheses (reviews in Møller and Pomiankowski 1993; Hebets and Papaj 2005). While the interactions between multiple signaling traits may differ across species, multiple signals may also evolve via selection on multi-trait displays acting as functional units (Hebets and Papaj 2005).

In birds, female preference for the elaborate songs and plumage of males is well described (Andersson 1994). However, because most studies focus on a single sensory domain (vocal, visual), the processes affecting the relative expression of song and plumage are poorly understood (Shutler and Weatherhead 1990; de Repentigny et al. 2000; Badyaev et al. 2002; Ornelas et al. 2009). Some studies indicate that female selection for one trait will eventually displace the other trait in a given environment (Shutler and Weatherhead 1990; Badyaev et al. 2002), whereas others suggest that such traits may be redundant (Møller and Pomiankowski 1993; Møller et al. 1998; de Repentigny et al. 2000). Alternatively, song and plumage signals may reflect different parameters of individual condition (Read and Weary 1992; Schluter and Price 1993; Iwasa and Pomiankowski 1994), or be unrelated (Ornelas et al. 2009).

In North American passerine birds, sub-adults from more than 30 species from at least eight families exhibit delayed plumage maturation (DPM), a delay in the attainment of their definitive adult plumage (Rohwer et al. 1980; Studd and Robertson 1985). Despite numerous hypotheses for DPM, there is no consensus about its function and adaptive benefits (Cucco and Malacarne 2000; Karubian et al. 2008). Young birds (usually males) in species with DPM have dull or female-like plumage throughout their first year (Rohwer et al. 1980). In most instances, such young males are sexually mature and able to reproduce during their first breeding season, although their reproductive success is typically much lower than adults (Ficken and Ficken 1967; Rohwer et al. 1980; Omland and Sherry 1994; Pavne 1982; Muehter et al. 1997). Although delayed expression of sexual signals in otherwise sexually mature males is found in a number of taxa including lizards (Martín and Forsman 1999) and primates (Setchell 2003), results from bird studies contribute to the majority of our understanding of how sexual signals change over an individual's lifetime.

In a review of age-related signaling in birds, Cucco and Malacarne (2000) suggested that DPM may reflect a more generalized delay in sexual signaling traits. In a comparison of 137 Western Palearctic passerines, the authors found that for the 29 species where data were available, eight exhibited a distinct song in their first breeding season and underwent significant changes (predominantly through additions/deletions to their song repertoire) between their first and second years, whereas 21 did not. They termed those species in which the songs of first-year birds differ significantly from those of older birds, but adult song does not change with age, as undergoing delayed song maturation (DSM). Cucco and Malacarne (2000) noted that of the eight species exhibiting DSM, seven also exhibited DPM. Although the observed co-occurrence between song and plumage signaling traits is intriguing, the authors cautioned that studies demonstrating a clear difference in song between yearling and adult males are relatively scarce. More research is needed to understand both the proximate basis and adaptive/evolutionary significance of DSM. While the mechanisms underlying DSM are unclear, learning almost certainly plays a central role. Here, we use the term DSM in a manner consistent with previous work (Cucco and Malacarne 2000) to describe species exhibiting a significant difference between the songs of first-year and older birds, with little or no change to song features in subsequent years. Our usage of the term does not imply that observed song changes must necessarily result from maturation; such changes may also be the outcome of processes such as vocal production learning.

The majority of studies considering age-based changes in song examine additions or deletions to song repertoire between the first and second breeding seasons, particularly in large-repertoire species (e.g., Kiefer et al. 2006, 2009). Recent studies have begun to accumulate examples of agebased changes in performance-related structural song traits (reviewed in Kipper and Kiefer 2010); however, very few have included species with marked DPM (but see Cucco and Malacarne 1999). If DPM and DSM do co-occur, and the delayed maturation of one signaling trait is due to a generalized delay in signal development, as theorized by Cucco and Malacarne (2000), we would predict a relationship between the relative expression of each signaling trait. The most obvious way to test for such a relationship is a comparison of the song and plumage traits associated with delayed maturation. This could help determine if birds of either age class with a more adult-like expression of one trait show similar levels of development in the other (positive association), or if expression of one signaling trait comes at the expense of the other (trade-off). Alternatively, comparing each signaling trait with pairing and reproductive success may offer insight into the selective pressures (costs/benefits) of expressing a more developed signal and may help elucidate the targets of female mate choice in species with multiple sexual signals. Although several studies have investigated plumage and reproductive success in yearling males with DPM (e.g., Greene et al. 2000; Karubian 2002), our understanding of how differences in adult/yearling song might be reflected in the reproductive success of species with delayed signaling development is limited. Furthermore, because song functions in dual roles (mate choice and territorial defense) in many species, past studies examining age differences in song changes may not have been able to distinguish the significance of such changes to neighboring males and

females. Therefore, it is useful to examine the relation between DPM and DSM in a species where songs directed at females are clearly discernable from those directed at conspecific males.

The American redstart (Setophaga ruticilla) offers an ideal model for comparing age-related development in male plumage and song-based sexual signals. American redstarts are a highly ornamented, sexually dichromatic species of Parulid warbler, which exhibits marked DPM. Adult males (after-second-year, ASY) are predominantly black (melanin pigment-based plumage), with orange coloration on their wings, tail, and flanks (Sherry and Holmes 1997). Yearling (sub-adult, second-year, SY) males appear female-like during their first winter and breeding seasons and are greenish-gray with yellow plumage coloration instead of the orange of adult males on the wings, flanks, and tail. The orange/yellow plumage of American redstarts is carotenoid pigment-based (McGraw et al. 2005), and recent work indicates that color variation in adult males is associated with mate choice (Reudink et al. 2009a; Germain et al. 2010a) and winter territory acquisition (Reudink et al. 2009b). Individual variation in yearling male plumage can also be pronounced; some yearling males exhibit various degrees of adult-like orange coloration in their normally vellow plumage regions and/or exhibit irregular patches of adult-like black plumage (primarily on the head and breast) as a result of adventitious feather loss (Rohwer et al. 1983; Sherry and Holmes 1997).

Song may also differ between yearling and adult male American redstarts. The repertoire of this species, like many closely related Parulid warblers, contains two distinct song categories that are used in different social contexts: repeat and serial song (Ficken and Ficken 1965; Lemon et al. 1994; Staicer et al. 2006). Repeat song (one song sung continuously in repetitive manner) is widely thought to function in mate attraction for Parulid warblers (Kroodsma 1981; Kroodsma et al. 1989). Repeat song in American redstarts is sung more commonly early in the breeding season before and during female arrival, whereas serial songs are more commonly used later in the breeding season during male-male aggressive territorial interactions (Ficken and Ficken 1965; Lemon et al. 1985, 1987; Staicer et al. 2006). Serial songs can be comprised of all notes and remaining (other than repeat) song types in an individual's repertoire and are sung with immediate variety. Although adult male redstarts can change their serial song repertoire by adding and deleting new notes and songs from year to year to match those of neighbors (Ficken and Ficken 1965; Lemon et al. 1985, 1987, 1994); Lemon et al. (1994) determined that birds were more likely to make changes to their repertoires after their first year than in subsequent years. Age-related changes in repeat song of redstarts, however, have not been documented. Most male American redstarts conform to the typical repeat song described in Lemon et al. (1987); however, the composition (here defined as the distinct notes which comprise an individual's song) of repeat song may vary considerably between individuals (Fig. 1), and some males may incorporate notes into their repeat song that are used in the serial repertoire of others (Lemon et al. 1985, 1987). Once males acquire territories during their first breeding season, the composition of repeat song typically remains unchanged from year to year (i.e., males do not add or delete repeat song notes across years, Lemon et al. 1994). Some evidence suggests that yearling males sing repeat songs at a higher rate than adults (Tourangeau 2002; but see Procter-Gray and Holmes 1981; Staicer et al. 2006), but no study has investigated the structural aspects of repeat song in the American redstart across age classes or determined the aspects of repeat song which may be involved in pairing and reproductive success.

In this study, we compared the structure and delivery of repeat (mate-attraction) songs in yearling and adult males to determine whether American redstarts exhibit delayed song maturation. No differences in repeat song across age class would indicate that age-based differences in song are limited to the territorial (serial) song type in this species. We then tested for a correlation between the relative expression of "adult-like song" and "adult-like plumage" for males in each age class. If a more adult-like expression of one signaling trait corresponds to a more adult-like expression in the other, this would be consistent with a generalized delay in signal development, whereas a negative correlation would suggest there is a trade-off. Finally, we examined individual variance in both song and plumage signals to determine predictors of pairing success and onset of breeding in both age classes as well as realized reproductive success in adult males.

Methods

Field work was conducted during the 2007–2008 breeding seasons (May through July) at the Queen's University Biological Station in south-eastern Ontario, Canada (44°34'N, 76°19'W). We walked daily transects across the 100-ha study site to determine arrival date and breeding status for all individual color banded adult (2007, n=54, 2008, n=47) and yearling (2007, n=15, 2008, n=14) males. Arrival date was calculated as the number of days after the arrival of the first male each season to standardize across years (Reudink et al. 2009c). We monitored each male for 20–30 min/day to determine pairing status and onset of breeding (date of social partner's first egg). Date of first egg was standardized across years in the same manner as arrival date. We recorded songs of adult (2007, n=19, 2008, n=24) and yearling (2007, n=9, 2008, n=14) males for 20 min within 24–36 h after arrival



Fig. 1 Repeat song examples from four adult and four yearling male American redstarts, illustrating repeat song diversity between and within age class. Numbers represent phone categories: l=first category syllable (FCS), 2=high frequency sweep (HFS), 3=terminal accent note (TAN). Although most males exhibit repeat songs similar

to either the first and second song examples for each age class, the two males W/P, Y/A1 and Bk/W, Bk/A1 illustrate extreme examples of males incorporating notes into their repeat song typically used as components of serial song in other males

on their territory, using a Marantz PMD670 digital recorder (recordings saved as .wav files) and an Audiotechnica directional microphone. All songs were recorded within a distance of 6–8 m from the focal male. Recording sessions took place between 06:00 and 10:00 EDT during the period of male arrival, from May 4th–June 18th of each year. If a newly arrived male was first discovered later in the day, we recorded songs the following morning. For a subset of males (adult, n=5, yearling, n=5), multiple 20-min recording bouts were sampled opportunistically over a 4-week interval (mean±SD=4.2±1.03 recordings/male, 5.83 ± 2.59 days between recordings from same male) to test for repeatability in repeat song structure across the breeding season.

In 2008, we also conducted weekly transects across a series of 30–40 ha study plots unconnected to the main study site (separated by \geq 3 km), where yearling males (n= 10) were recorded opportunistically. In these distant plots, we could not accurately determine arrival date for any of the ten males and could only determine mating status for one. Following song recording, we captured all males (both main and peripheral plots) on their territories using mist nets accompanied by a decoy and song playback, and

marked each bird with both a Canadian Wildlife Service aluminum band and a unique combination of three color bands. Males were aged following Pyle (1997), where the rumps of yearling males are dark gray and contrast with the pale gray back, while uniformly black adult males have no distinct color contrast between the back and rump.

From each bird, we recorded unflattened wing chord length (millimeters) as a measure of relative body size (Reudink et al. 2009a, b) and plucked both a single tail feather (rectrix 3) and 12–15 flank feathers. We classified adult male bib size in hand using a 1–5 scale developed by Lemon et al. (1992). In addition, in 2008, we photographed yearling male breast and head plumage (4–5 pictures/individual) on a gridded background in a series of standard poses to quantify the amount of black plumage present in each region.

While several previous studies of American redstarts have used genetic paternity as the main measure of reproductive success in adult males (e.g., Perreault et al. 1997; Reudink et al. 2009c), a large proportion of yearling males fail to attract mates (Ficken 1962; Lemon et al. 1987; Lozano et al. 1996). Of 21 yearling males with known mating status in our study population (2007–2008), only 7 (33%) attracted females, only 4 (19%) had dates of first egg that were recorded, and of these only one achieved paternity for at least one chick (M. Reudink, unpubl. data). Therefore, following Lozano et al. (1996), we used pairing status (presence/absence of a female building a nest on the male's territory), rather than date of first egg or paternity, as the measure of "success" for yearling males.

In the subset of adult males included in this study (n=9,all 2007) for which full measures of realized (genetic) reproductive success were previously assessed (Reudink et al. 2009a, c), we used total within-pair paternity and total genetic offspring fledged as measures of reproductive success. Paternity analyses (storage, extraction, amplification, assignment) follow Reudink et al. (2009c). Briefly, paternity analysis was conducted using five microsatellite loci (Dpµ01, Dpµ03, Dpµ05, Dpµ15, Dpµ16) originally isolated from yellow warblers, Dendroica petechial (Dawson et al. 1997). Over the 4 years of study in which paternity was assessed, Reudink et al. (2009c) analyzed DNA from 265 offspring from 75 nests and all putative parents. Total withinpair paternity was calculated as the number of offspring sired at the primary and secondary (if polygynous) nests, and total genetic offspring fledged as the number of fledged offspring from both within-pair nesting attempts and extra-pair young.

Song analysis

Song recordings were digitized at a sampling rate of 22,050 Hz (16 bit format), and analyzed using the Syrinx sound analysis program (Burt 2005). For each song measured, we used a fixed resolution of 1.5 ms, and we recorded frequency measures to ± 0.01 kHz and time measures to ± 0.01 s. All variables of fine song structure were measured manually using the time and frequency

cursor (following Foote et al. 2008) by the same observer (RRG), and information about singer's age was masked during analysis by using band number to code the sound files. Each recording contained on average 87.3% ($\pm 7.6\%$) vocalizations classified as repeat songs, where the remaining vocalizations were either single-note calls or "chips" (vocalizations made while fighting with an intruding male). Songs were considered repeat songs if they met all three of the following criteria: (1) were those sung early in the breeding season, before and during female arrival (Lemon et al. 1985, 1987), (2) were sung repeatedly and continuously throughout the focal recording, and (3) matched the focal recording (both by ear and sound spectrogram) on successive days when the birds were visited. We analyzed 20-min recording bouts from a total of 74 individuals for which we had both plumage and vocal data (adult, 2007= 19, 2008=24; yearling, 2007=9, 2008=22). Any deviations from these sample sizes in further analyses are due to missing data points for given variables and are described throughout. We recorded and analyzed only one 20-min singing interval from each male, as repeat song structure in this species has been shown to be consistent throughout the breeding season for adult males (Lemon et al. 1994). We confirmed this result across age class using a subset of individuals by comparing all song structural variables (Table 1) from two recordings (>14 days apart) during the same season (adult, n=5, yearling, n=5, two-tailed t test, all p > 0.34). From each 20-min recording bout, we calculated song rate (number of songs/min) and subsequently analyzed the highest quality (i.e., least amount of background or overlap noise) songs (mean±SD=33±13 songs/bird out of a mean 138±52 songs/recording) for seven measures of song structure (Table 1). These measures included duration (seconds), number of first category syllables (#FCS),

Table 1 Mean±SD of song rate, consistency, and ten structural measures of male American redstart repeat song (adult=43, yearling=31)

Variable	Abbreviation	Adult males	Yearling male	
Song rate (songs/min)	Rate	6.45±2.69	7.70±2.36	
Song duration (s)	Duration	1.10 ± 0.14	1.03 ± 0.15	
Coefficient of variation duration	CV duration	$0.10 {\pm} 0.12$	$0.06 {\pm} 0.05$	
Number of first category syllables used in most frequent repeat song	FCS	4.55±1.13	$4.37 {\pm} 0.85$	
Inverse proportion of total repeat songs that are non-standard in length ^a	Consistency	29.13 ± 52.95	30.31 ± 44.46	
Bandwidth of last first category syllable (kHz)	BW-FCS	$2.41 {\pm} 0.53$	$2.74 {\pm} 0.62$	
Bandwidth of high frequency sweep (kHz)	BW-HFS	$0.78 {\pm} 0.66$	$0.63 {\pm} 0.55$	
Bandwidth of terminal accent note (kHz)	BW-TAN	2.99 ± 1.42	$2.92{\pm}1.44$	
Bandwidth of whole song (kHz)	BW-whole	$4.63 {\pm} 0.53$	$4.66 {\pm} 0.64$	
Coefficient of variation-bandwidth of whole song	CV-whole	$0.06 {\pm} 0.05$	$0.06 {\pm} 0.03$	
Frequency at maximum amplitude (kHz)	FMA	$7.11 {\pm} 0.46$	$7.36{\pm}0.59$	
Coefficient of variation-frequency at maximum amplitude	CV-FMA	$0.07 {\pm} 0.03$	$0.07 {\pm} 0.03$	

^a Calculated as the inverse ratio of songs which had additional/fewer first category syllables (than the most frequent version of the song) to the total number of songs

bandwidth (kilohertz) of last first category syllable (BW-FCS), bandwidth (kilohertz) of high frequency sweep (BW-HFS), bandwidth (kilohertz) of terminal accent note (BW-TAN), bandwidth (kilohertz) of the entire song (BWwhole), and the frequency (kilohertz) at maximum amplitude (FMA) (Fig. 1). In addition to mean measures of individual song characteristics, we quantified the ability of males to deliver stereotyped songs by calculating mean coefficients of variation (CV) for song duration, frequency at maximum amplitude, and bandwidth of the entire song (Table 1). Finally, we calculated the overall consistency of individual male repeat song by dividing the number of songs which had additional/fewer first category syllables than the normal (most frequent) version of the song by the total number of songs. These ratios were then divided by 1 to produce the reported "consistency" values. We considered song rate and consistency as behavioral measures of repeat song, and therefore did not include them in discriminant function analysis of repeat song structure.

Plumage analysis

Standardized photos of 21 yearling males were uploaded into Adobe[®] Photoshop[®] CS3 (v. 10.0) and analyzed following Germain et al. (2010b). Briefly, we measured the area of black (adult-like) plumage on the head (from behind bill to nape, including lores, hereafter called head) and breast (chin, throat, and breast, hereafter called breast) and calculated the total area (square millimeter) of black plumage visible on the breast and head of each yearling male, controlling for body size.

Preparation and spectrophotometric analysis of collected feathers from both yearling and adult males followed Reudink et al. (2009a), using an Ocean Optics USB4000 spectrometer (Dunedin, FL, USA) attached to a PX-2 pulsed xenon light source. We took 25 readings throughout the orange (adult) or yellow (yearling) region of both flank and tail feathers, and gathered reflectance data into 1 nm bins using CLR 1.03 (Montgomerie 2008). We also calculated the extent of tail color patch size by measuring the area (square millimeter) of yellow/orange color patches on both sides of the rachis of collected tail feathers using digital calipers (±0.01 mm). This measure was then divided by the total area of the tail feather to control for feather size. In instances where the color patch on tail feathers was too small to gather accurate reflectance readings (adult, n=5, yearling, n=6), or not enough flank feathers were collected (adults only, n=2), we excluded that feather region from spectrophotometric analysis. This yielded a final sample of 35 adult and 24 yearling males with song and tail reflectance spectra data, and 38 adult and 30 yearling males with song and flank reflectance spectra data. To calculate the brightness of each plumage region, we averaged the percent reflectance from 320–700 nm. We then calculated the standard variables of hue, UV chroma, and red chroma (saturation) using color equations described in Germain et al. (2010b), adapted from Montgomerie (2006).

Statistical analysis

All statistics were performed using JMP 8.0.1 (SAS Institute 2009) and R 2.10.1 for Windows (R Development Core Team 2009). In instances where data were collected for the same individual across 2 years (n=4 adults in both years, n=0 yearling-to-adult resamples), we randomly excluded data from 1 year (determined by coin flip) to avoid pseudoreplication. Data on morphology and song were pooled across both years of study and tested for year effects using t tests. Feathers collected in 2007 had previously undergone spectrophotometric analysis as part of several other studies on American redstart ornamentation. To remove any variance associated with year that might be due to feather degradation from repeated measurements, we centered plumage color values by year with a series of one-way ANOVAs (each color variable versus year) and used the residuals from these tests in subsequent analysis. All variables were tested for equal variance (Levene's homogeneity of variance test) and normality (Shapiro-Wilks test) before use in further analysis.

Age-based song and plumage separation

We used Pearson's correlation analysis to examine all song structure and all plumage variables for multicollinearity. For variables found to be highly collinear (i.e., $r \ge 0.7$: McGarigal et al. 2000), we calculated univariate ANOVAs for each variable and compared their F values. Variables with the highest F value were retained while those with lower F values were excluded from further analysis (Noon 1981; Herring et al. 2008). In addition, we used Mahalanobis distance outlier analysis to identify multivariate outliers (song n=3, plumage n=0), which may represent birds with unusual song features unlikely to be part of the population of song features we wish to describe (Quinn and Keough 2002) and were subsequently excluded from discriminant analysis.

Song variables with non-normal distributions (CVduration, consistency, BW-FCS, BW-HFS, BW- TAN, BW-whole, and CV-whole) were transformed (log10, third root, log10, square root, square root, square root, log10, respectively). Four of these transformed variables (log10 CV-duration, $\sqrt{BW-HFS}$, $\sqrt{BW-TAN}$, $\sqrt{BW-whole}$) still failed to meet the assumptions of normality. However, because non-normality in each of these cases was due to skewness and not outliers, these transformed variables may still be entered into discriminant analysis and the resultant significance tests are reliable (Tabachnick and Fidell 1996; Quinn and Keough 2002). Linear discriminant function analysis (DFA) was then used to determine the best single or combination of song structural characteristics that separated males by age, using age class as the classification variable, and nine non-collinear measures of song structure (duration, CVduration, FMA, CV-FMA, BW-FCS, BW-HFS, BW-TAN, BW-whole, CV-whole) as predictor variables.

Most plumage variables fit the assumptions of normality, except the standardized area of black head and breast plumage on yearling males and flank hue (yearling and adult males). We transformed black head and black breast plumage by taking the square root of each variable. However, flank hue was not transformed, as (1) it was centered by year (residuals from univariate ANOVA, year as independent variable) and thus contains a proportion of individuals with negative values for this measure, and (2) the non-normal distribution was once again due to skewness and not significant outliers. For plumage-based DFA of all males, we used age class as the classification variable and six non-collinear measures of carotenoid coloration for all males (tail color patch size, tail brightness, tail red chroma, flank brightness, flank hue, flank red chroma) as predictor variables.

Interactions of song and plumage

We performed an ANCOVA between song and plumage canonical variate scores (obtained from DFA of plumage and song variables, respectively) with age as a co-variate to determine if, overall, individuals with more "adult-like" song structure also had more "adult-like" plumage. In addition, we conducted a series of linear regressions to determine if song canonical score was related to the melanin-pigment based plumage of adult (bib score) and yearling (extent of adult-like black plumage) males, and if plumage canonical score was related to singing behavior.

Predictors of pairing and reproductive success

Predictors of pairing success (binary response of mated/ unmated) were determined using a series of nominal logistic regressions, with backwards stepwise elimination, that were separated based on (1) age, morphology, and arrival date, (2) song structure and singing behavior, and (3) plumage coloration. Because yearling black breast and head plumage data were collected only in 2008, we excluded these variables from multivariate analysis. Instead, we used *t* tests to determine if there was a significant difference in the amount of black breast and head plumage between paired and unpaired yearling males. We used *t* tests to compare summary measures of song and plumage (canonical variate scores) between paired and unpaired males of each age class. We then compared date of first egg for adults with individual plumage and song variables using a series of multiple regressions with backward stepwise deletion and canonical variate scores with linear regressions, respectively. Finally, we compared the individual song and plumage characteristics of a small subset of adult males (n=9, all from 2007) for which we had full measures of genetic reproductive success (total within-pair paternity and total genetic offspring fledged) using a series of linear regressions. Because of the small sample size for adult male realized reproductive success, we reduced the number of variables in this analysis by including only the song and plumage characteristics found to differ between yearling and adult males (those significantly correlated with canonical scores obtained from discriminant analysis).

All tests were two-tailed (equal variance), and all models were tested using Akaike's information criterion (AIC) to ensure that final models were the most parsimonious. Table-wide sequential Bonferroni corrections were applied to control for the number of tests used.

Results

Year effects and age differences

Adult male American redstarts captured in 2008 had larger relative body size (wing length, $R^2=0.16$, $t_{37}=2.63$, p=0.01) than those captured in 2007. Yearling males captured in 2007 had higher song rates ($R^2=0.13$, $t_{28}=-2.09$, p=0.05) and tended to have earlier standardized arrival on the breeding grounds than those captured in 2008, although the difference was not statistically significant ($R^2=0.18$, $t_{18}=2.00$, p=0.06). Across age classes, adult males had longer wing length (ANCOVA, year as covariate, $F_{2,63}=28.65$, p<0.0001) and arrived earlier ($R^2=0.47$, $t_{58}=7.18$, p<0.0001) than yearling males.

Age-based song and plumage separation

A DFA significantly separated the structure of adult and yearling American redstart repeat song based on canonical variate scores (R^2 =0.21, t_{65} =4.16, p<0.0001; Fig. 2a) and predicted age class with 79.1% accuracy (29/37 adult males, 24/30 yearling males). Canonical variate scores were significantly negatively correlated with song duration (R^2 =0.13, $F_{1,65}$ =9.68, p=0.003), CV duration (R^2 =0.10, $F_{1,65}$ =6.96, p=0.01), and BW-HFS (R^2 =0.06, $F_{1,65}$ =4.02, p=0.05), and significantly positively correlated with both FMA (R^2 =0.27, $F_{1,65}$ =23.53, p<0.0001), and BW-FCS (R^2 =0.43, $F_{1,65}$ =49.50, p<0.0001). In other words, the repeat songs of individuals with higher (more "yearling-like")



Fig. 2 Box plots of (a) repeat song canonical variate score for adult male (n=37) versus yearling male (n=30) repeat song, and (b) plumage canonical variate scores for adult male (n=35) versus yearling male (n=24) American redstarts. *Horizontal lines* represent the median, 10th, 25th, 75th, and 90th percentiles, respectively

canonical scores were characterized by: (1) shorter mean song duration, and more stereotyped song duration, (2) higher mean FMA, (3) larger mean FCS bandwidth, and (4) smaller mean HFS bandwidth. Yearling males tended to sing more songs per minute than adult males, although this relationship was not significant (ANCOVA, year as covariate, $F_{2,67}=2.74$, p=0.07).

For song behavior within each age class, males with more consistent songs had lower CV-duration in both adult ($R^2=0.33$, $F_{1,38}=18.49$, p=0.0001) and yearling males

 $(R^2=0.67, F_{1,28}=56.36, p<0.0001)$. Yearling males with more consistent songs tended to have lower CV-whole, although this relationship was not statistically significant $(R^2=0.12, F_{1,28}=3.95, p=0.06)$. In other words, both yearling and adult males who were most consistent in the number of first category syllables included in their songs also had the least variation in song duration, as expected. Adult males with higher song output rate had larger BW-WHOLE $(R^2=0.17, F_{1,38}=7.63, p=0.009)$. No other song structure variables were related to either measure of singing behavior (all p>0.14).

The plumage coloration of adult and yearling males differed significantly, based on DFA canonical variate scores for all males ($R^2=0.87$, $t_{57}=19.38$, p<0.0001; Fig. 2b). These scores predicted age class with 100% accuracy (35/35 adult males, 24/24 yearling males). Across age class, plumage canonical variate scores increased with increasing tail brightness ($R^2=0.08$, $F_{1,57}=4.77$, p=0.03), flank brightness ($R^2 = 0.28$, $F_{1.57} = 22.60$, p < 0.0001), and flank hue $(R^2=0.91, F_{1.57}=566.12, p<0.0001)$, and decreased with tail color patch size ($R^2=0.17$, $F_{1.57}=$ 11.58, p=0.001), tail red chroma ($R^2=0.61$, $F_{1.57}=89.47$, p < 0.0001), and flank red chroma ($R^2 = 0.59$, $F_{1.57} = 80.61$, p < 0.0001). Thus, the overall carotenoid coloration of individuals with higher (more "vearling-like") canonical variate scores were characterized by: (1) a smaller relative area of coloration on the tail feather, (2) tail feathers that were brighter and less saturated with red/orange pigment, and (3) flank feathers that were brighter, less saturated with red/orange pigment, and more "yellow-like" in hue. There were no significant relationships between carotenoid canonical score and either bib score in adult males or the area of black plumage on the breast or head of yearling males (all p > 0.35).

Interactions of song and plumage

While plumage and song canonical variate scores were significantly positively correlated in the pooled sample of adult and yearling males (Fig. 3), this relationship was predominantly due to age, which was the only significant predictor of plumage and song score (ANCOVA, age as covariate, $F_{3,52}$ = 7.25, $p_{\text{plumage}}=0.10$, $p_{\text{age}}=0.002$, $p_{\text{age*plumage}}=0.41$). Variance of both song and plumage scores did not differ across age class, and variance did not differ between signaling traits within each age class (all p > 0.17). We found no significant relationships between plumage canonical score and measures of singing behavior (song rate, consistency) in either age class or between song canonical score and bib score in adult males (all p > 0.38). Similarly, in yearling males, we found no relationship between song canonical score and the extent of adult-like black on head or breast plumage (all p > 0.17).



Fig. 3 Song and plumage canonical scores for adult (*solid circle*) and yearling (*open circle*) male American redstarts. Each axis extends from lower "adult-like" scores to higher "yearling-like" scores. While song and plumage scores are correlated across age class (R^2 =0.15, $F_{1,54}$ = 9.82, p=0.003), there is no linear relationship between the two traits within adult (R^2 =0.02, $F_{1,30}$ =0.48, p=0.5) or yearling males (R^2 =0.10, $F_{1,22}$ =2.34, p=0.14)

Predictors of pairing and reproductive success

Logistic regression of pairing success using all males revealed, as expected, that age class was the strongest predictor of pairing success (Table 2). Because of the strong relationship between age and wing length ("year and age differences", above), relative body size was not entered into the model of age, morphology, and arrival date. Due to the strong effect of age on pairing success (Table 2), we also separated models by age class to determine whether any of the tested predictors of pairing success differed across age. When separated by age, both BW-FCS and FMA song

variables were associated with pairing success in adult, but not yearling, males (Table 2). Post-hoc analysis of these variables revealed that paired adult males had lower mean FMA (two-tailed t test; $R^2 = 0.11$, $t_{37} = -2.18$, p = 0.04), and larger BW-FCS (two-tailed t test; $R^2=0.11$, $t_{37}=2.10$, p=0.04) than unpaired adult males, where the latter result is inconsistent with the previous result (Table 2) of larger BW-FCS being a more yearling-like song trait. After tablewide Bonferroni correction (α =0.001), only age remained a significant predictor of pairing success. T tests revealed no significant difference in plumage or song canonical scores between paired and unpaired males of either age class (all p > 0.32). In addition, there was no significant difference between paired (n=4) and unpaired (n=8) yearling males in the amount of either black breast plumage or black head plumage (two-tailed t tests, both p > 0.35).

Stepwise regressions comparing date of first egg with individual measures of adult plumage coloration and song revealed that adult males with duller and less saturated tail feathers began nesting earlier (Table 3), although only tail brightness was significant after table-wide correction (α = 0.003). There were no significant predictors of date of first egg with individual measures of song structure or singing behavior. Comparisons of date of first egg with overall plumage and song development (canonical scores) revealed that song score was a significant predictor of onset of breeding, where adult males with more adult-like song scores began nesting earlier (R^2 =0.26, $F_{1,16}$ =5.59, p= 0.03), but that there was no relationship between plumage score and date of first egg (p=0.77).

Linear regressions of adult realized reproductive success with plumage and song variables that significantly contributed to age-based separation of each trait (six correlates of plumage canonical score, song rate, and five correlates of song canonical score) revealed that males which fledged a greater number of total genetic offspring had lower mean FMA (R^2 =0.57, $F_{1,7}$ =9.37, p=0.02). This relationship,

 Table 2
 Final models of nominal logistic regressions examining pairing success in relation to age, arrival date, plumage coloration, and song structure/behavior using stepwise backward deletion

		Predictor variables	β	SE	χ^2	р	
All males	Age, arrival date (final model, $\chi^2 = 14.25$, $n = 60$, $p = 0.0002$)	Intercept	-0.41	0.31	1.76	0.19	
		Age	-1.11	0.31	12.61	0.0004	
Adult Song variables (final model, $\chi^2 = 11.15$, $n = 39$, $p = 0.004$)	Song variables (final model, $\chi^2 = 11.15$, $n = 39$, $p = 0.004$)	Intercept	-12.74	8.82	2.08	0.15	
	BW-FCS	-20.70	10.31	4.03	0.04		
		FMA	2.54	1.24	4.16	0.04	
Yearling	Song variables (final model, $n=21$)	No significant predictors					
Adult	Plumage coloration (final model, $n=39$)	No significant predictors					
Yearling	Plumage coloration (final model, $n=21$)	No significant predictors					

Adult males had significantly greater pairing success than yearlings. Within adults, birds with lower frequencies at maximum amplitude and higher bandwidths of the first category syllable paired more successfully

	Predictor variables	В	F	р
Song variables (final model <i>n</i> =21)	No significant predictors			
Plumage variables (final model, $R^2 = 0.41$, $F_{2,16} = 5.52$, $p = 0.02$)	Tail brightness	1.85	9.76	0.007
	Tail red chroma	455.69	5.96	0.03

Table 3 Final models of multiple regressions examining standardized date of first egg in relation to male plumage coloration and song structure/ behavior, using stepwise backward deletion

however, was not significant after sequential Bonferroni correction (α =0.002). In addition, adult males which sired more within-pair offspring tended to have lower mean FMA (R^2 =0.35, $F_{1,7}$ =3.77, p=0.09) and decreased flank red chroma (R^2 =0.34, $F_{1,7}$ =3.57, p=0.10), although these differences were not significant. Comparisons of adult realized reproductive success with overall plumage and song scores revealed no significant relationship between realized success and repeat song canonical score (p=0.84), and a marginally significant relationship with plumage canonical score (R^2 =0.44, $F_{1,7}$ =5.55, p=0.051).

Discussion

In this study, we analyzed the structure of mate-attraction (repeat) songs across age class in the American redstart and found that the repeat songs of young males differed significantly from those of adults. We determined that a more adult-like song was correlated with an earlier onset of breeding in adult males and that two of the structural features of repeat song that most significantly contributed to its separation across age class (frequency at maximum amplitude and bandwidth of the first category syllable) were correlates of adult pairing and genetic reproductive success (before Bonferroni correction). Individual variables of adult and yearling plumage were not linked with pairing or reproductive success but were associated with onset of breeding in adult males. Although the exact nature of the relationships between the structural aspects of repeat song and reproductive success are unclear (i.e., adult pairing success correlated with one adult-like and one yearling-like song trait) and require experimental tests, our results provide the first evidence, to our knowledge, of delayed maturation of a song type used principally during mate attraction in a species with delayed plumage maturation.

We are not aware of any study since Cucco and Malacarne's (2000) investigation that has specifically addressed the relationship between plumage ornamentation and song in yearling males of a species with DPM. Combined with previous evidence of delayed maturation in serial song of American redstarts (Lemon et al. 1994), our finding of a small yet significant age-based separation in repeat song indicates that DSM can occur in different song types used in different contexts during the breeding season. Although playback experiments are needed to determine whether male and female redstarts perceive these differences between yearling and adult repeat songs, our results concur with the prediction that DSM is more likely to occur in species with DPM (Cucco and Malacarne 2000). However, contrary to the predictions of Cucco and Malacarne (2000), we did not find evidence that the delayed maturation of one signaling trait may represent a more generalized delay in the development of secondary sexual signals.

The development of repeat song in American redstarts has not been studied and so the roles of learning from others and practice in song maturation is unknown. Adult males do not change their repeat song from year-to-year to copy those of neighbors (Lemon et al. 1994), and neither adults (Lemon et al. 1994) nor yearlings (this study) appear to change their repeat song throughout the breeding season. In contrast to this lack of information on repeat song learning, detailed work by Lemon et al. (1994) shows that male redstarts make significant changes to their serial song repertoire between their first and second breeding seasons, but not as frequently in subsequent years, mainly as a result of males copying (through additions or deletions of two or more songs) the serial songs of their neighbors, forming song neighborhoods. Longitudinal studies of repeat song recorded from individual males as yearlings and adults could provide useful insights into the song development process. Additionally, such studies could clarify whether the marginally significant higher song rates of yearlings that we detected were due to breeding status (mostly unpaired subjects) rather than age. For example, while Staicer et al. (2006) reported higher repeat song rates in unpaired than paired male American redstarts of both age classes, neither that study nor Procter-Gray and Holmes (1981) found significant age effects on song rate.

In comparing how song and plumage varied with reproductive success, we found that adult male redstarts with more adult-like repeat songs began breeding earlier each season than those with more yearling-like songs. In addition, adult males with lower mean frequencies at maximum amplitude (a more adult-like song characteristic) had greater pairing success and fledged more genetic offspring (though the latter result was not significant following Bonferroni correction). The emergence of this pattern despite a small sample size suggests that variation in repeat song is associated with breeding success and provides support for the role of repeat song in female mate choice, which while historically predicted, has yet to be explicitly tested in American redstarts. Interestingly, while age-based song score was correlated with timing of breeding in adult males, we found no relationship between song canonical score and genetic reproductive success, despite associations between this measure of success and individual adult male song characteristics. These patterns suggest that while repeat song may function in mate attraction, its role in extra-pair behavior may be limited, compared to that of plumage coloration (Reudink et al. 2009a).

With respect to plumage, both adult male tail brightness and tail red chroma were associated with first-egg date, where adult males with duller and less saturated feathers bred earlier. Earlier onset of breeding is typically found to have a strong positive influence on annual reproductive success, both in this population (Norris et al. 2004) and many passerine species (reviewed in Dunn 2004). While less saturated tail feathers in adults may be indicative of older, more experienced adult breeders (Reudink et al. 2009a), previous studies have found adult males with brighter tails arrive earlier on the breeding grounds and are more likely to be polygynous and that flank coloration is more strongly associated with paternity in American redstarts, based on larger sample sizes (Reudink et al. 2009a, b).

We did not sample the territorial (serial) songs of males to compare with reproductive success, and it is important to note that territory quality may also play an important role in female mate choice. The acquisition of high-quality territories, presumably influenced by earlier arrival dates, may be more strongly related to male age, plumage coloration, and winter territory quality (Reudink et al. 2009a, b, c) than to serial song types sung later in the breeding season (Lozano et al. 1996), but additional studies are needed to make direct comparisons. Future work should also seek to determine if individuals differentially delay the development of different song types (serial vs. repeat song) during their first year, as the benefits of sounding more adult-like to females through repeat song may be augmented by sounding more yearling-like (and less threatening) to conspecific males through serial song.

Overall, we detected a stronger coupling of pairing and genetic reproductive success with individual measures of song, rather than plumage, in this age-based set of comparisons (e.g., Table 2), and that canonical scores of adult-like song and plumage are each associated with some measure of "success" during the breeding season (song scores with onset of breeding, plumage scores with realized reproductive success). Adult and yearling male American redstarts are easily identified based on their plumage characteristics, which are very distinct (Fig. 2b). In this age-biased mating system, ornamental adult plumage coloration has previously been shown to be a correlate of individual male quality (Reudink et al. 2009a). While repeat songs are significantly different between age classes (Fig. 2a), there is less separation between yearling and adult males in this signal and a greater potential for individuals of one group to be statistically misidentified to the other based on their song. Therefore, there may be a greater pressure for males of each age class to sound more adult-like than to look more adult-like. By expressing a more adult-like song, yearling males could provide a more current indicator of individual condition during the timing of mating (as opposed to timing of molt with plumage), allowing females to better assess male quality based on several signaling traits (Cucco and Malacarne 2000). We were unable to directly test these ideas in this study, due to the relatively small number of successfully paired yearlings (n=7 over 2 years ofmonitoring), and the relatively low return rates of males banded as yearlings in this system (none in this study, approx. 9% from 2001 to 2008, L. Ratcliffe, unpubl. data).

Monitoring yearling male success over additional years, especially in years of lower adult density, will be required to better determine the influence of song and/or plumage on female mate choice decisions as they influence yearling reproductive success. For example, in a long-term study of indigo buntings (Passerina cyanea), first-year males that matched the individual songs of local adults and were able to maintain territories near their song models had greater mating success, were in higher-quality habitats, and were better able to defend their territories from intruders (Payne 1982; Payne et al. 1988). Further, Payne (1982) showed that first-year males with more adult-like blue plumage also had greater pairing/nesting success, and those which expressed both bluer plumage and matched the songs of local adults could achieve the success levels of adult males. The potential benefits of adult-like signaling are echoed in several studies focusing on only one signaling trait, which demonstrate that having more adult-like song is advantageous for young males (Hasselquist et al. 1996), as is plumage that appears more adult-like (Karubian 2002). Alternatively, several theories predict that reduced aggression by adult males leads to greater access to females for subadult males with less-developed secondary sexual traits (Rohwer et al. 1980; Lyon and Montgomerie 1986; Foster 1987). Additionally, in some cases, there is evidence of disruptive selection for yearling appearance, as in lazuli buntings (Passerina amoena), where yearling males with the brightest (adult-like) and dullest (female-like) plumage were more successful (i.e., defending high-quality territories, pairing, siring offspring) than those with intermediate plumage (Greene et al. 2000).

We did not detect any relationship between the degree of adult-like song and adult-like plumage expressed by males of either age class (Fig. 3), suggesting that song and plumage signaling traits may be unrelated in this species. These findings are similar to those of Ornelas et al. (2009) who detected no evidence of either an association or tradeoff between acoustic and visual signaling in trogons (Trogonidae). Of these two potential alternative outcomes, trade-offs between song and plumage traits are more likely than positive correlations within wild populations, as energetic resources are likely to be normally distributed (Shutler 2011). Although several studies have tested for trade-offs between song and plumage, there is limited evidence for their prevalence (Shutler and Weatherhead 1990; Badyaev et al. 2002; Ornelas et al. 2009; Shutler 2011). Plumage coloration has been advocated as an important mate choice signal in this species, particularly with respect to achieving polygyny and retaining withinpair paternity (Reudink et al. 2009a); however, the role of repeat song in mate choice is less well known. Our results suggest that individual variation in American redstart repeat song does play a role in female mating decisions, but the specific targets of female choice for this signaling trait remain unknown. While further investigations are necessary to elucidate the interactions between song and plumage signaling traits, and experimental evidence is needed to directly test the response by females to variation in each trait across age groups, our results illustrate an age-based separation in the mate-attraction song of the species, and support the notion that investment in sounding more adultlike may be beneficial for yearling males.

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Ethical standards Experiments in this study comply with the current laws of the countries in which they were performed.

Conflict of interest The authors declare that they have no conflict of interest.

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