

Relationships between carotenoid-based female plumage and age, reproduction, and mate colour in the American Redstart (*Setophaga ruticilla*)

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Abstract: Most studies investigating the function and evolution of ornaments have focused on males. Variation in ornaments may also reflect individual quality and convey information in females. We examined correlations between female plumage colour and reproductive variables in the sexually dichromatic songbird, the American Redstart (*Setophaga ruticilla* (L., 1758)). Female American Redstarts display yellow, carotenoid-based plumage patches on their tails, wings, and flanks. Using reflectance spectrometry, we quantified brightness (feather structure) and “yellowness” (hue and chroma) of tail and flank feathers to examine whether female plumage colour varies with age, reproductive success, parental care, and the plumage colour of mates. Female plumage varied with age, with adult (after-second-year) females having brighter tail feathers than first-year females. We failed to find a relationship between female plumage colour and pairing or first-egg dates. However, adult females with brighter tails visited their nests less frequently and first-year females with brighter tails fledged fewer offspring. Adult females with brighter tails also mated with males who provided less care. In addition, adult females with yellower flanks paired with males with brighter flanks and with males who provided less parental care. We suggest that plumage colouration in female American Redstarts can act as a signal of individual age and quality.

Key words: American Redstart, carotenoid, colour, female ornament, plumage, *Setophaga ruticilla*, sexual selection.

Résumé : La plupart des études sur la fonction et l'évolution des ornements se sont intéressées aux mâles. Les variations des ornements des femelles pourraient également refléter la qualité des individus et transmettre de l'information. Nous avons examiné les corrélations entre la couleur du plumage des femelles et des variables relatives à la reproduction chez la paruline flamboyante (*Setophaga ruticilla* (L., 1758)), un oiseau chanteur caractérisé par un dichroïsme sexuel. Les femelles de cette espèce présentent des zones de plumage jaune à base de caroténoïde sur leur queue, leurs ailes et leurs flancs. Nous avons quantifié la clarté (structure de la plume) et le caractère jaune (tonalité et saturation) de plumes de queue et de flanc par spectrométrie par réflectance afin de déterminer si la couleur du plumage des femelles varie selon l'âge, le succès de reproduction, le soin parental et la couleur du plumage du compagnon. Le plumage des femelles variait selon l'âge, les femelles adultes (après la deuxième année) présentant des plumes de queue plus claires que les femelles d'un an. Nous n'avons trouvé aucun lien entre la couleur du plumage des femelles et le moment de l'appariement ou des premiers œufs. Toutefois, les femelles adultes présentant une queue plus claire visitaient leur nid moins fréquemment et les femelles d'un an présentant une queue plus claire produisaient moins d'oisillons envolés. Les femelles adultes avec une queue plus claire s'accouplaient également avec des mâles faisant preuve de moins de soin parental. En outre, les femelles adultes présentant des flancs plus jaunes s'accouplaient avec des mâles avec des flancs plus clairs et des mâles faisant preuve de moins de soin parental. Nous postulons que la coloration du plumage des femelles de la paruline flamboyante peut constituer un indice de l'âge et de la qualité individuels. [Traduit par la Rédaction]

Mots-clés : paruline flamboyante, caroténoïde, couleur, ornement de la femelle, plumage, *Setophaga ruticilla*, sélection sexuelle.

Introduction

The historic tendency to view female ornaments as evolutionary products of natural selection for crypsis and genetic correlation with males (Lande 1980, 1987; Amundsen 2000; Amundsen and Parn 2006; Potti and Canal 2011) has recently been challenged. The emerging consensus is that selection on females is not always for crypsis, and that selection and genetic correlation are not mutually exclusive alternatives. The relative importance of selection and genetic correlation in shaping female ornaments

remains unclear (Kraaijeveld et al. 2007; Clutton-Brock 2009). Only by investigating the potential of female ornaments to act as inter- and intra-sexual signals will we understand the mechanisms of male mate choice, status signaling, and the evolution of sexual mono- and di-morphism.

Males invest less in reproduction than females and hence compete more strongly for mates, which drives the evolution of showy male display traits (Darwin 1871; Bateman 1948; Trivers 1972). Showy traits can reduce the costs of male–male competition and

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allow males to signal their quality to females (Andersson 1994). Because males and females share the majority of the genome, females typically possess some aspect of the male display. However, females often compete less strongly for mates, and therefore their inherited ornaments may serve no benefit and be reduced by natural selection for crypsis (Lande 1980). The predicted outcome of this sexually antagonistic selection is sexual dimorphism, with females less ornamented than males (Lande 1980; Cox and Calsbeek 2009).

Competition between females can increase selection for female ornaments (LeBas 2006; Rosvall 2011). If females compete among themselves for sexual or nonsexual resources, then signals of quality could be used to avoid conflict. Hence, the evolution of female ornaments could reduce the costs of competition (injuries, time spent fighting), a traditional explanation for male ornaments. For example, meerkat (*Suricata suricatta* (Schreber, 1776)) females invest more in reproduction than males; a situation traditional sexual selection theory predicts will lead to male–male competition for mates and hence more ornamented males. However, the increased parental investment by females leads to strong female–female resource competition, and female display traits are used to reduce the cost of this competition (Clutton-Brock et al. 2006). Resource competition between females is also moderated by ornaments in the Rock Sparrow (*Petronia petronia* (L., 1766)), where females with larger yellow plumage patches access food earlier (Griggio et al. 2010). Similarly, strong female–female competition for nest sites may explain the dramatically reversed sexual dichromatism in parrots of the genus *Ecliptus* Wagler, 1832 (Heinsohn et al. 2005).

Male mate choice is another process that can promote the evolution of female ornaments. Although male mate choice is considered less prevalent than female–female competition (LeBas 2006), it is increasingly recognized as a common phenomenon (Edward and Chapman 2011). Males may prefer females with traits reflecting increased reproductive capability (Servedio and Lande 2006). In some species, female appearance changes with age (Morales et al. 2007; Bitton et al. 2008; del Val et al. 2010), allowing males to discern females that have previous breeding experience. Additionally, if these traits indicate the level of care a female may provide to offspring (Linville et al. 1998), males may adjust parental input to maximize the quality of care to offspring while minimizing energy output (Burley 1986; Roulin 1999). Even when female–female competition is minimal, as is often the case in lekking species, males may still exhibit some degree of choosiness and thereby drive the evolution of female ornaments (Saether et al. 2001). Direct evidence for male mate choice has been found in mate choice trials (Amundsen et al. 1997; Griggio et al. 2009).

It is important to note that a relationship between female appearance and an aspect of individual quality (such as age, size, or reproductive success) does not demonstrate the existence of functional female ornaments, female–female competition, or male mate choice, because the relationship could be driven by other processes such as a genetic correlation with males. The relation between appearance and individual quality does, however, demonstrate a potential signaling function for female ornaments.

Avian plumage is commonly used to study sexual selection (e.g., Hill and McGraw 2006). Although sex-based differences in plumage have been used as proxies for the strength of sexual selection on males (Shutler and Weatherhead 1990; Owens and Hartley 1998; Dunn et al. 2001; Badyaev and Hill 2003), females of both monomorphic and dimorphic species can exhibit traits that are equally “flashy” (e.g., plumage colour of bee-eaters (family Meropidae), waxwings (genus *Bombycilla* Vieillot, 1808), and toucans (family Ramphastidae)) or condition-dependent (e.g., carotenoid-based plumage patches, long tails), or that present a predation risk through contrast with their environment (Amundsen and Parn 2006). In natural populations, primary evidence for plumage acting as a sexual signal or quality-indicating trait in females may be

observed through relationships between plumage expression and condition or immunocompetence (Andersson 1994; Hórák et al. 2001; Piersma et al. 2001; Massaro et al. 2003), age (Stutchbury and Robertson 1987; Komdeur et al. 2005; Morales et al. 2007; but see Linville et al. 1998), survival (Hórák et al. 2001), maternal and paternal care (Linville et al. 1998; Smiseth and Amundsen 2000; Matessi et al. 2009), or reproductive success (Massaro et al. 2003; but see Jones and Montgomerie 1992). Although not definitive evidence, assortative mating by plumage (Jawor et al. 2004; MacDougall and Montgomerie 2003; Griggio et al. 2005) is expected when female plumage indicates quality (Kraaijeveld et al. 2007). The most direct evidence for plumage acting as a metric of quality is a relationship between plumage ornamentation and lifetime reproductive success. However, when variance in reproductive success is low and sample sizes are limited, researchers often examine fitness-related variables such as pairing and first-egg dates as working proxies for reproductive performance (e.g., Ninni et al. 2004; Halfwerk et al. 2011; Cauchard et al. 2012).

Here, we examine correlations between female plumage and reproductive variables in the sexually dichromatic, but mutually ornamented American Redstart (*Setophaga ruticilla* (L., 1758)). Expression of yellow–orange carotenoid-based plumage traits, like those exhibited by American Redstarts, is condition-dependent in many species and variation in these traits may act as an indicator of individual quality (Hill and McGraw 2006). Carotenoid-based colour has two components: feather structure and carotenoid density. Feather structure is thought to determine brightness, while carotenoid concentration determines colour “intensity” (Saks et al. 2003; Shawkey and Hill 2005). Brightness may therefore signal individual condition and colour intensity may signal both condition and foraging ability (Endler 1983), though further work is needed to clarify the influence of these factors on American Redstart colour expression. In American Redstarts, male plumage is correlated with parental care, winter habitat quality, the probability of mating, and reproductive success and therefore appears to be under selection in both the breeding and the non-breeding seasons (Reudink et al. 2009a, 2009b; Kappes et al. 2009; Germain et al. 2010). More specifically, on our study site in southeastern Ontario, females were found to provide less care when mated with males with more intensely red tails, while offspring of males with brighter flanks received more care from both parents (Germain et al. 2010; but see Kappes et al. 2009). During the non-breeding season, males with brighter tails inhabit higher quality winter territories, a key driver of arrival timing on the breeding grounds (Marra et al. 1998; Reudink et al. 2009b). Early arrival on the breeding grounds is associated with higher reproductive success through higher rates of polygyny and extra-pair paternity (Reudink et al. 2009b). Flank redness is also associated with male-realized reproductive success, where individuals with redder flanks secure more within-pair paternity (Reudink et al. 2009a).

In this study, we examine the potential for female plumage to indicate individual quality in free-living American Redstart females by testing if the colouration of carotenoid-based regions of female tail and flank plumage is related to age, parental care, and metrics of reproductive success. If female colour is selected for as it is in males, we predict female tail brightness to be correlated with reproductive variables, such as pairing date and total fledged, and female flank brightness and “redness” (here “yellowness”) to be correlated with provisioning. In addition, we assess the potential for assortative mating with respect to both plumage and parental care. If there is no relationship between female colour and reproduction, parental care, or the plumage colour of mates, this would suggest the plumage colour of female redstarts is the result of genetic correlation with males (Lande 1980), as suspected in many species (reviewed in Nordeide et al. 2013).

Materials and methods

Study species

American Redstarts are single-brooded, open-cup nesting, long-distance neotropical migratory songbirds. The species is socially monogamous, but facultatively polygynous and sexually promiscuous (Sherry and Holmes 1997). Female American Redstarts exhibit yellow, carotenoid-based patches on the wings, tail, and sides of breast (flanks), and display these patches during copulation solicitation (Sherry and Holmes 1997; M.W. Reudink, personal observation). Adult (after-second-year or ASY) male American Redstarts exhibit the same plumage pattern as females, but are black-orange as opposed to the grey-yellow patterning of female and yearling (second-year or SY) males. Juveniles of both sexes undergo a partial moult on or near the natal grounds, moulting body feathers but not tail and flight feathers, which are retained throughout the subsequent breeding season. A complete moult occurs following each subsequent breeding season (Sherry and Holmes 1997). It is therefore important to note that while tail feathers of ASY birds may represent individual condition or foraging ability at the time of moult, SY tail feathers are grown while nestlings are still being fed by their parents. Thus, SY tail feather colouration is influenced both by individual quality and condition, as well as the quality of parental provisioning.

Field data collection

Field data were collected at the Queen's University Biology Station, southeastern Ontario, Canada (44°34'N, 76°19'W), from 1 May to 31 July, 2005–2007. American Redstarts were captured in mist nets using song playback combined with model decoys (taxidermic mounts) to simulate territorial intrusions. Females were also lured into mist nets with a playback of fledgling distress calls (recorded in our study area). Birds were banded with a US Geological Survey (USGS) aluminum band and a unique combination of three colour bands for individual identification. One tail feather (third rectrix or R3) and 12–15 feathers from the center of the yellow-orange portion of the flanks were collected from each bird. To reduce the invasiveness of our study, we did not pluck any primary feathers, which also have carotenoid-based yellow-orange patches. Individuals were aged as SY or ASY; SY males having grey-yellow plumage as opposed to the black-orange plumage of ASY males, and SY females having smaller yellow patches on the R3 and less wear on the retrices (Pyle 1997).

From 1 May to 15 June, we conducted daily transects of the study area between 0600 and 1200 EST. Males arriving on breeding grounds immediately begin singing and are easily detected. Females typically begin to arrive several days after the first males arrive and begin nest-building shortly after pairing. Pairing date was noted as the date a female was detected by a change in male behaviour (e.g., following, whisper-singing) and visual confirmation of the presence of the female. Once individuals paired, we conducted daily focal observations (generally ~30 min) to record first-egg date, clutch size, hatching success, and fledging success. Because eggs and chicks are frequently predated, the same pair often re-nests multiple times. Reproductive variables were reported from only the clutch that successfully fledged. In cases where a pair was unsuccessful in fledging young, reproductive variables were reported from the last nest that held a clutch or hatched (for additional details see Reudink et al. 2009a, 2009c). We banded nestlings 5 days after hatching. Once nests were located, we conducted additional focal observations every 1–2 days throughout the season to detect polygynous mating. Only the primary (first) nest of polygynous males was used in subsequent analyses (see below). Because male American Redstarts exhibit delayed plumage maturation, and pairing and fledging success is

greatly reduced in SY males (Ficken and Ficken 1967; Lozano et al. 1995), we limited our study to females paired with ASY males.

Feeding rates and nest attendance

We monitored parental care by males and females at 32 nests in 2006 and 2007 ($n = 13$ in 2006, $n = 19$ in 2007). As detailed by Germain et al. (2010), video cameras (Canon ZR500) positioned >5 m from the base of the nest tree recorded the number of nest visits and total time at the nest by the male and female during a 120 min period between 0600 and 0900 EST 5 and 7 days after hatching. Both the number of visits and the time at nest are positive indicators of parental effort in small insectivorous birds (Saetre et al. 1995; but see Moreno et al. 1997). To control for effects of human disturbance on parental behaviour during camera setup, we discarded the initial 5 min of each recording prior to analysis. We also divided visits to the nest and time at the nest for each parent by the number of offspring to standardize rates of parental care by brood size (Smiseth et al. 2001). Mean brood size over the 2 years was 3.25 (SD = 0.91). Comparing standardized parental care variables (effort-h⁻¹-chick⁻¹) to the raw data (effort-h⁻¹) revealed that both variables were highly positively correlated and representative of total parental effort (Germain et al. 2010). For polygynous males with parental care observations ($n = 7$), only the first nest was included in analyses. Neither maternal or paternal care differed between nests of monogamous males ($n = 23$) and the first nests of polygynous males (female time at nest: $t = -0.49$, $P = 0.63$; female visits to nest: $t = 1.01$, $P = 0.32$; male time: $t = 0.95$, $P = 0.35$; male visits: $t = 1.05$, $P = 0.31$).

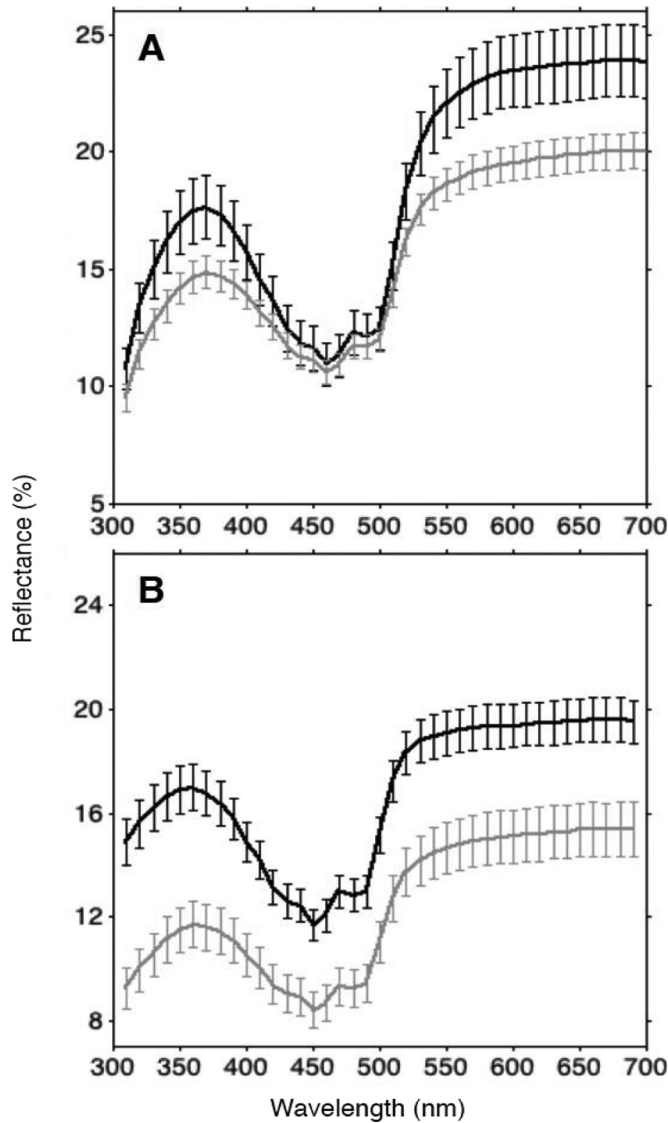
Colour analyses

We measured variation in the carotenoid-based tail and flank colouration of 59 females ($n_{SY} = 30$, $n_{ASY} = 29$); 13 of which we measured flank colouration only ($n_{SY} = 6$, $n_{ASY} = 7$) because small yellow patches precluded accurate measures of tail colour. To quantify plumage colouration, we followed the same techniques used for males (for detailed methods see Reudink et al. 2009a and Germain et al. 2010; see also the supplementary material¹). Values for male tail and flank colour are from Reudink et al. (2009a) and Germain et al. (2010). Briefly, we used reflectance spectrometry to quantify plumage reflectance across the songbird visual spectrum (320–700 nm). We then calculated values for brightness (mean light reflected across the spectrum) and used principal components analysis (PCA), on the tail and flank separately, to quantify variation in the shape of the curve and produce a variable (PC1) that represented hue and chroma¹. PCA was used to avoid multiple testing and to remain consistent with previous studies (e.g., Reudink et al. 2009a; Germain et al. 2010). The first principal component, PC1, was positively correlated with hue (tail: $r_{[55]}^2 = 0.09$, $P = 0.03$; flanks: $r_{[55]}^2 = 0.08$, $P = 0.03$) and red chroma (tail: $r_{[55]}^2 = 0.74$, $P < 0.0001$; flanks: $r_{[55]}^2 = 0.81$, $P < 0.0001$), and negatively correlated with UV chroma (tail: $r_{[55]}^2 = 0.53$, $P < 0.0001$; flanks: $r_{[55]}^2 = 0.57$, $P < 0.001$). Thus, females with higher PC1 values appear a more intense yellow (“yellower”), which corresponds to what Reudink et al. (2009a) and Germain et al. (2010) call a higher “redness” in males.

Although we controlled for brightness when calculating PC1 values, when including both ASY and SY females tail PC1 and tail brightness were negatively correlated ($t = -2.9$, $P = 0.006$, $n_{SY} = 16$, $n_{ASY} = 21$). Because tail PC1 is an orthogonal variable and is more complex than tail brightness alone, we chose to remove tail PC1 from analyses with both ASY and SY females to avoid multicollinearity, and retained the variable of tail brightness. No other colour variables were correlated.

¹See also the supplementary material, which is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0017>.

Fig. 1. Mean (\pm SE) reflectance spectra for (A) flank and (B) tail feathers of female American Redstarts (*Setophaga ruticilla*). After-second-year (ASY) females are represented by the thick black line (flanks: $n = 28$; tail: $n = 23$), whereas second-year (SY) females are represented by the grey line (flanks: $n = 30$; tail: $n = 24$).



Statistical analyses

We first built a linear mixed-effect model (LME; all analyses performed in R version 2.9.1; R Development Core Team 2009) to assess whether any of the three uncorrelated female colour variables (tail brightness, flank brightness, and flank PC1) differed between the two female age classes. To control for random effects related to repeated sampling of returning birds, we included the random effect of bird identity. We compared variance components to assess the effect of returning birds.

We then built linear models (LM) to assess whether the female colour variables (tail brightness, tail PC1, flank brightness, and flank PC1) described patterns in (i) pairing date, (ii) first-egg date, (iii) number of chicks fledged, and (iv) level of parental care. Because colour differed between age classes (see Results; Fig. 1), we ran analyses of female colour relations (with pairing date, first-egg date, parental care, and number fledged) separately for each age class. We did not include bird identity as a random effect in these models because no birds were sampled multiple times in the same age class. We then performed two-sample t tests to look for differ-

Table 1. Significant and nonsignificant (NS) relationships between response variables and uncorrelated color variables of second-year (SY) and after-second-year (ASY) female American Redstarts (*Setophaga ruticilla*).

Response variable	Tail		Flank	
	Brightness	PC1	Brightness	PC1
Female age	$z = 2.64^{**}$	—	NS	NS
Pairing date	NS	NS	NS	NS
First-egg date	NS	NS	NS	NS
Fledging success	$t = -3.10^{**}$ (SY)	NS	NS	NS
Maternal care	$t = -2.40^*$ (ASY)	NS	NS	NS
Paternal care	$t = -2.59^*$ (ASY)	NS	NS	$t = -3.01^*$ (ASY)
Mate flank brightness	NS	NS	NS	$F = 11.73^{**}$ (ASY)

Note: *, $P < 0.05$; **, $P < 0.01$.

ences between age classes. For all LM and LME, we set $\alpha = 0.05$ and used backwards stepwise regression.

Next, we asked if parental care patterns of pairs were related using pairwise linear regression on male and female parental care variables. We used the same approach to then investigate the existence of assortative mating with respect to colour; we performed pairwise linear regression on male and female colour variables. In both cases, we used a Bonferroni correction to control for multiple testing ($\alpha = 0.013$ and $\alpha = 0.004$, respectively).

Ethical standards

Research was conducted under Queen's University Animal Care and Use Committee guidelines (protocol No. Reudink-2005-007) and under Canadian Wildlife Service collection permit No. CA 0154 and banding permit No. 10766C. The experiments described comply with the laws of Canada.

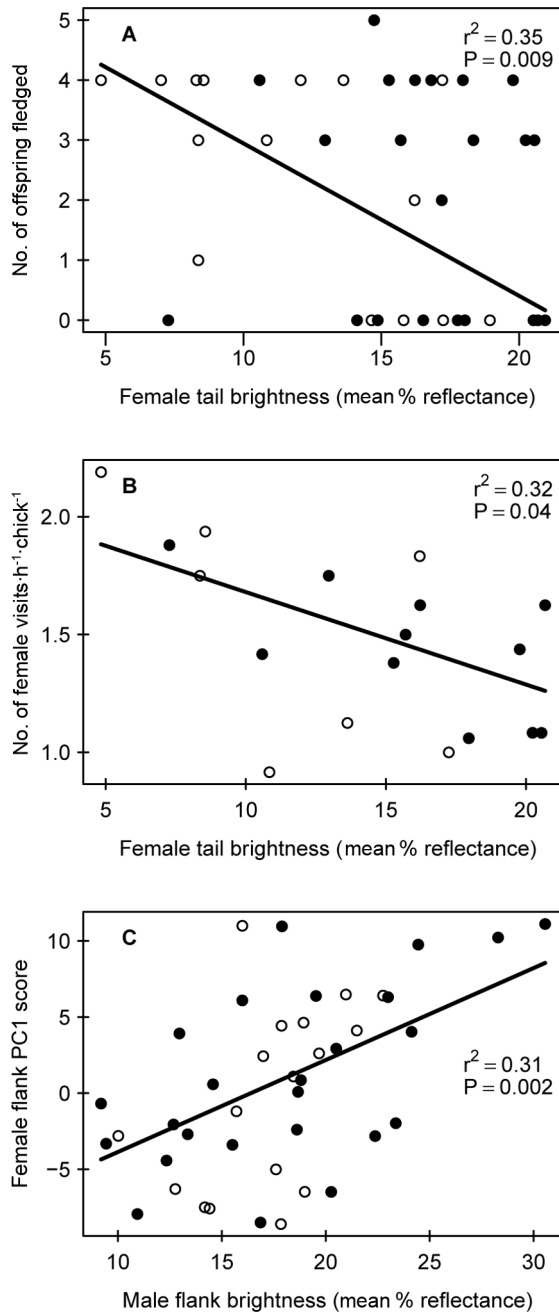
Results

When we examined differences in plumage colouration between SY and ASY females, we found that ASY females had brighter tails than SY females ($z = 2.64$, $P = 0.008$, $n_{SY} = 16$, $n_{ASY} = 21$; Table 1, Fig. 1). There were no age differences in flank brightness or flank PC1 (neither variable retained in final model). The random effect of individual was negligible compared with the intercept (SD of random effect smaller than SD of intercept), implying that repeated sampling of returning birds ($n = 2$) did not influence the results.

Pairing date and first-egg date were not modeled adequately by any predictive variable associated with female colouration for either age class. However, a model with flank and tail brightness described 41% of the variation in fledging success for SY females ($F_{[2,13]} = 6.29$, $P = 0.01$), indicating that SY females with brighter tails fledged less offspring ($t = -3.10$, $P = 0.009$; Table 1, Fig. 2A). Neither pairing date ($t = -1.04$, $P = 0.30$, $n_{SY} = 30$, $n_{ASY} = 47$), first-egg date ($t = -0.92$, $P = 0.36$, $n_{SY} = 27$, $n_{ASY} = 41$), nor number fledged ($t = -1.03$, $P = 0.31$, $n_{SY} = 28$, $n_{ASY} = 44$) differed between female age classes.

The number of visits ASY females made to the nest declined with tail brightness, which described 32% of the variation ($F_{[1,9]} = 5.78$, $P = 0.04$, $t = -2.40$; Table 1, Fig. 2B). Neither tail nor flank colour described parental care provided by SY females ($n = 7$). A model with all four female colour variables approached significance, explaining 56% of the variation in the number of visits an ASY's mate made to the nest ($F_{[4,6]} = 4.23$, $P = 0.06$) and indicating that males made fewer visits when mated to ASY females with yellower flanks ($t = -3.01$, $P = 0.02$; Table 1). A model with tail PC1 and brightness also approached significance, explaining 33% of the variation in the time an ASY female's mate spent at the nest ($F_{[2,8]} = 3.49$, $P = 0.08$) and indicating that males mated with ASY females with brighter tails spent less time at the nest ($t = -2.59$, $P = 0.03$; Table 1). Male parental care was not significantly described by SY plumage colour ($n = 10$). Neither maternal care (visits:

Fig. 2. (A) Second-year (SY) female American Redstarts (*Setophaga ruticilla*) (open circles) with brighter tails fledged fewer offspring. There was no relationship between tail brightness and fledging success with ASY females (solid circles). Line of best fit is shown for SY females. (B) After-second-year (ASY) females with brighter tails visited the nest less often. There was no relationship between tail brightness and nest visits with SY females. Line of best fit is shown for ASY females. (C) ASY females with yellower flanks mated with males with brighter flanks. There was no evidence of assortative mating by colour in SY females. Line of best fit is shown for ASY females.



$t = 1.53$, $P = 0.14$; time: $t = 0.55$, $P = 0.58$; $n_{SY} = 7$, $n_{ASY} = 11$) nor paternal care from the mate (visits: $t = 1.57$, $P = 0.13$; time: $t = 1.24$, $P = 0.23$; $n_{SY} = 7$, $n_{ASY} = 11$) differed between female age classes.

Parental care was significantly positively correlated in pairs with ASY females in three of four comparisons (female and male time at nest: $F_{[1,18]} = 14.18$, $P = 0.001$, $r^2_{\text{adjusted}} = 0.41$; female and male visits to nest: $F_{[1,18]} = 12.81$, $P = 0.002$, $r^2_{\text{adjusted}} = 0.38$; female visits to

nest and male time at nest: $F_{[1,18]} = 11.44$, $P = 0.003$, $r^2_{\text{adjusted}} = 0.35$). Male parental care was not significantly correlated with parental care by SY females ($n = 10$).

When we examined patterns of assortative pairing by plumage colouration, we found that ASY females with yellower flanks were more likely to pair with males that had higher flank brightness values ($F_{[1,23]} = 11.73$, $P = 0.002$, $r^2_{\text{adjusted}} = 0.31$, $t = 3.424$; Table 1, Fig. 2C). No other colour variable was related to assortative mating in pairs with ASY females, and no patterns of assortative mating by colouration were found in pairs with SY females.

Discussion

In this study, we demonstrate that carotenoid-based plumage traits of female American Redstarts are associated with age, maternal care, fledging success, and parental care and plumage of social mate (Table 1)—all important components of fitness. In addition, our predictions based on patterns found in male American Redstarts were supported: female tail brightness is correlated with reproductive success and female flank yellowness is correlated with provisioning. Surprisingly, however, these correlations are in opposite directions in males and females, suggesting that different aspects of plumage colour may be important in males and females.

While many studies demonstrate that carotenoid-based plumage patches act as condition-dependent indicators of individual quality in males (Hill and McGraw 2006), relatively few have examined plumage colouration as a metric of individual quality in females (Amundsen and Parn 2006). We suggest that plumage colouration in female American Redstarts can play a functional role as an indicator of individual age and quality, though these patterns appear to be quite complex and age-dependent. For example, older females exhibit brighter tails, which could suggest that higher brightness is associated with higher quality individuals. However, within age classes, tail brightness is negatively correlated with fledging success in SY females and is negatively correlated with maternal and paternal care in ASY females. Thus, within age classes, tail brightness appears to be negatively associated with individual quality. Higher brightness values are often associated with lower carotenoid deposition, suggesting that lower brightness values may actually indicate higher foraging efficiency and (or) condition during moult. This explanation is difficult, however, as Reudink et al. (2009a, 2009b) found increased tail brightness in males to be positively correlated with both winter habitat quality and probability of polygyny.

One explanation for the differences in plumage colouration between SY and ASY females are moult patterns. Hatch-year American Redstarts of both sexes undergo a partial moult on or near the breeding grounds, moulting body feathers, including flank feathers. However, flight feathers, including tail feathers, begin growing while still in the nest and are not replaced prior to migration (Sherry and Holmes 1997). Tail feathers expressed by SY and ASY females are therefore grown under very different conditions, with SY females acquiring most or all nutrients and carotenoids for feather growth and colour through parental provisioning. Thus, while tail colouration in ASY females may be an honest indicator of individual condition, foraging ability, and time available for moult (Serra et al. 2007), tail colouration in SY females is influenced by parental provisioning, as well as individual quality and condition (Evans and Sheldon 2012). The absence of age-specific differences in female flank colour aligns with this hypothesis. While moult patterns are one possible explanation for our results, this is clearly a complicated system that requires a great deal of future exploration.

ASY females have brighter tail feathers than SY females, which could allow competing females and potential mates to assess age and experience. Although not found here, a recent study with a larger sample size found that ASY females arrive on the breeding

grounds and lay their first egg earlier than SY females (Porter 2012). Males may therefore be able to increase their fitness by selectively mating with ASY females. In our study, we found positive assortative mating with respect to age (Fisher's exact test: $P = 0.018$, $n = 95$).

Tail brightness also varied with reproductive success in SY females, and maternal care in ASY females, and could therefore indicate parental ability. It is possible that males respond to this signal, as paternal care declined with female tail brightness. In contrast, female flank colour did not vary with age, but was related to male colour and levels of paternal care in pairs with ASY females. Males may therefore also be responding to the colour of female flanks.

The observation of age-specific differences in females is consistent with other passerines, such as Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)) (Robertson et al. 1992) and Brazilian Tanagers (*Ramphocelus bresilius* (L., 1766)) (Nogueira and Alves 2008), which exhibit age-specific differences in plumage colour and iris colour, respectively. Similarly, Morales et al. (2007) demonstrated that older female Pied Flycatchers (*Ficedula hypoleuca* (Pallas, 1764)) are more likely to exhibit a white forehead patch characteristic of males. While females exhibiting the white forehead patch raised more fledglings, reproductive success was not related to age per se, suggesting that the white forehead patch may indicate female quality but not necessarily previous breeding experience (Morales et al. 2007). A similar age-related change in plumage colouration was observed in American Redstart ASY males (Reudink et al. 2009a). Reudink et al. (2009a) found that tail redness (equivalent to PC1 values measured in this study) decreased as ASY males aged, possibly due to increased reflectance in the UV region of the spectrum and an associated rise in the blue-green "trough" of the reflectance spectrum. In other words, rather than a decrease in carotenoid-content in the feathers of older birds, changes in plumage colouration in older birds may be indicative of increased reflectivity in shorter wavelength regions of the spectrum, consistent with increased quality of the feather microstructure (which would also result in the increased brightness observed in tail feathers; Saks et al. 2003). Regardless of the mechanism involved, age-based variation in female plumage presents a mechanism through which male mate choice and female-female competition could act.

Female colour failed to explain pairing and first-egg dates, and although we did not find relationships between plumage colouration and reproductive success in ASY females, reproductive success was lower in SY females with brighter tails. Given that bright tails were found to be characteristic of ASY females, this result is perplexing. One possibility is that females with brighter tails provide less parental care, a pattern we found in ASY females (Fig. 2B). Smaller sample sizes may have precluded our ability to detect a significant relationship in SY females. In addition, low variance in female reproductive success or high rates of predation, or other limitations in sample size, may have hindered our ability to detect a direct relationship between plumage colour and fledging success in ASY females.

When we examined patterns of female plumage colouration and male provisioning, we found that ASY females with brighter tails and yellower flanks tended to pair with males who provided less parental care. Our data also provide evidence of assortative mating with respect to colour: ASY females with yellower flanks paired more often with males with brighter flanks. Interestingly, previous work in our population demonstrated that offspring of males with bright flanks received more care from both parents (Germain et al. 2010). Explaining these contrasting results requires further study.

The existence of relationships between female colour and age, maternal care, fledging success, parental care, and plumage of the social mate suggest that plumage colouration in female American Redstarts can act as a signal of individual age and quality. Further

studies, especially male mate choice experiments, are needed to test the functional role of American Redstart female plumage colouration in sexual communication and to disentangle some of these conflicting patterns.

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