

Inter-annual variation in American redstart (*Setophaga ruticilla*) plumage colour is associated with rainfall and temperature during moult: an 11-year study

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Abstract Carotenoid-based colouration plays an important role in sexual signaling in animals as an honest indicator of individual quality during mate choice and competitive interactions. However, few studies have examined how natural variation in weather conditions influences inter-annual variation in the expression of ornamentation, potentially through affecting the dietary availability of carotenoids. In this study, we examine variation in the expression of carotenoid-based plumage colouration in relation to temperature and rainfall during the pre-moult and moulting period over 11 years in a population of American redstarts, *Setophaga ruticilla*, breeding in eastern Canada. We used reflectance spectrometry of tail feathers collected from male and female redstarts to relate feather colour with weather conditions the previous breeding season during the months over which redstarts are likely to moult

(June–September). At a population level, birds expressed feathers with higher red chroma and lower brightness in years following high July rainfall and low August temperature. The pattern was stronger in males, but was generally consistent across ages and sexes. Analyses of feathers from repeatedly captured birds indicated that the above patterns could be explained by individual change in feather colour. We suggest that higher rainfall during the moulting period may increase insect abundance and the availability of dietary carotenoids. This is among the first studies to show effects of weather conditions on a sexual signalling trait, which may have important consequences for sexual selection, mate choice, and the reliability of putative signals.

Keywords Plumage · Carotenoid · Climate · Long-term · Moult · Colour change

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Introduction

The evolution of ornaments in animals has long fascinated scientists interested in sexual selection and mate choice. The colourful plumage of birds, in particular, has attracted much attention, with hundreds of studies aimed at examining the function and evolution of ornamental traits in birds (Hill and McGraw 2006). These traits have been shown to function in inter- (reviewed in Hill 2006) and intra-sexual (reviewed in Santos et al. 2011) interactions, often acting as honest indicators of individual condition or quality. Carotenoid-based plumage in particular has garnered attention because carotenoid pigments, which are responsible for producing yellow, orange, and red plumage, cannot be synthesized de novo, but rather must be ingested as part of the diet (Hill and Montgomerie 1994). Thus, individuals must be capable of obtaining sufficient carotenoids during

moult through efficient foraging (Endler 1983; Hill 1992). In addition, because of the antioxidant properties of carotenoids and their importance for immune function, a trade-off exists whereby only individuals in good health and condition can afford to allocate carotenoids to both self-maintenance and the production of colourful plumage (Lozano 1994).

Because the display of colourful carotenoid-based plumage is based in large part on the dietary availability of carotenoids, habitat selection during moult may be an important factor determining plumage expression. For example, great tits (*Parus major*) reared in deciduous forests moulted more yellow plumage compared to individuals reared in coniferous forests (Slagsvold and Lifjeld 1985). Follow-up studies demonstrated that this difference was due primarily to comparatively low intake of carotenoid-rich caterpillars in coniferous forests (Partali et al. 1987). In a recent study, American redstart (*Setophaga ruticilla*) males on their tropical wintering grounds regrew tail feathers with significantly lower red chroma after an original tail feather (grown on the breeding grounds) was plucked (Tonra et al. 2014). As chroma generally reflects carotenoid content (Saks et al. 2003), the authors suggested the reduction in red chroma was likely due to a lack of dietary availability of carotenoids during the dry season in the Caribbean, which precluded the growth of high-quality plumage (Tonra et al. 2014).

Despite much research into the function and evolution of ornamental plumage, factors influencing annual variation in ornament expression have received relatively little attention. Though a number of studies have examined the role of reproductive trade-offs (Siefferman and Hill 2005; Doutrelant et al. 2012) and contracted moult periods (Griggio et al. 2009; Newton and Dawson 2011; Stutchbury et al. 2011) on the production of sub-optimal plumage colouration, less is known about how natural variation in climatic conditions influences population-level ornamentation, which may have important effects on inter- and intra-sexual signaling during both the over-wintering and subsequent breeding periods. For example, years of low primary productivity (as measured by Normalized Difference Vegetation Index, NDVI) on the African wintering grounds of European barn swallows (*Hirundo rustica*) were associated with shorter tails and subsequently later reproduction and smaller clutches (Saino et al. 2004).

For species that undergo a complete post-breeding moult, conditions and food availability at the period surrounding moult can be critically important for the acquisition of high-quality plumage (Hill and Montgomerie 1994; Hill 2000). Scordato et al. (2012) recently observed complex cross-generational effects of climatic conditions on the expression of a sexually selected trait (wing bar size) in male Hume's warblers (*Phylloscopus humei*). Wing bar

size was influenced by temperature both during spring and summer, with warm springs leading to larger wing bars and warm summers leading to smaller wing bars in the following breeding season. Variation in the expression of sexually-selected traits at the population level through variation in climate can have significant impacts on the intensity of sexual selection. For example, Cockburn et al. (2008) demonstrated that sexual selection in superb fairy-wrens (*Malurus cyaneus*) was much stronger when conditions were good, i.e. in years of high rainfall. Thus, evidence is mounting that understanding the impact of weather conditions on the expression of ornamental traits is important for understanding how sexual selection acts to shape variation in these traits.

In this study, we examined variation in plumage colouration in a population of American redstarts over an 11-year period to determine whether temperature and rainfall during juvenile feather growth and adult post-breeding moult influenced expression of a sexually-selected trait. In our study population of American redstarts breeding in Ontario, Canada, we have demonstrated that variation in plumage colouration appears to have important inter- and intra-sexual signaling functions. Adult (referred to as after-second-year, or ASY) males with brighter tails are more likely to be polygynous (Reudink et al. 2009a), and both flank and tail colouration are important predictors of extra-pair paternity (Reudink et al. 2009a) and offspring provisioning (Germain et al. 2010). In addition, female tail brightness is positively associated with age and negatively associated with parental care in ASY females and fledging success in first-year (referred to as second-year, or SY) females (Osmond et al. 2013). Finally, tail brightness in both SY and ASY males is associated with winter territory quality, suggesting a possible intra-sexual signalling function during the non-breeding season (Reudink et al. 2009b). However, the role of weather conditions in influencing population-level variation in plumage colouration remains unexplored.

We collected tail feathers from ASY and SY males and females breeding at our study site and related them to annual weather conditions over 11 years to determine whether: (1) variation in weather (temperature, rainfall) during nesting and/or moult predicted variation in plumage colour the following season, (2) these patterns were consistent across ages and sexes, and (3) these patterns could be explained by individual change in feather colour.

Materials and methods

Study species

American redstarts are small (7–8 g) migratory birds that exhibit delayed plumage maturation. All females,

and males throughout their first year (including their first breeding season), exhibit grey plumage, with yellow carotenoid-based patches on the tail, flanks, and wings. Adult males exhibit similar patterning, but are black with orange patches. Redstarts are insectivores that prey on Homoptera, Diptera, Coleoptera, Lepidoptera, and Hymenoptera species, from which they obtain carotenoids needed for plumage production (Robinson and Holmes 1982). Juveniles (SY) begin growing tail and wing feathers while still in the nest, typically in June or July at our study site, and retain those feathers through the next breeding season (Pyle 1997). Adults (ASY) undergo a single post-breeding moult that generally occurs between July and September, usually just following successful or unsuccessful breeding attempts (Pyle 1997; Sherry and Holmes 1997).

Field methods

Fieldwork for this project was conducted at the Queen's University Biological Station (QUBS), Chaffey's Lock, ON, Canada (44°34'N, 76°19'W) from May to July 2001–2011. Male American redstarts were captured shortly after territory establishment using mist nets and simulated territorial intrusions (decoy with song playback). Females were captured during feeding trips to the nest or by luring into nets using playback of fledgling distress calls. All birds were banded with a unique combination of a single Canadian Wildlife Service aluminum band and 2–3 colour bands, then aged as either SY or ASY. Because redstart males exhibit delayed plumage maturation, male age was determined as SY if the males retained the juvenile grey/yellow plumage patterning or ASY if they exhibited definitive black/orange colouration. Females were aged SY/ASY based on the degree of wear and colouring on the rectrices and moult limits (Pyle 1997). From each individual, a single tail feather (3rd rectrix) was then plucked and immediately stored in a manila coin envelope and placed in a cardboard box to reduce light contamination prior to colour analysis in the laboratory. We observed no linear relationships between colour variables and year sampled, suggesting that time since plucking did not influence feather colour; similarly, little effect of feather age had previously been demonstrated with museum specimens, especially those collected within the past 50 years (Armenta et al. 2008).

Our analysis involved a total of 578 tail feathers from 481 individuals, including 193 ASY males, 72 ASY females, 176 SY males, and 65 SY females (Table 1). Fifty ASY individuals (46 males and 4 females) were present in >1 year (2.4 ± 0.7 years, range 2–4), and 25 SY individuals returned as ASYs in at least one subsequent year (2.2 ± 0.4 years, range 2–3).

Table 1 Annual sample sizes of American redstart (*Setophaga ruticilla*) feathers used in an analysis of the relationship between feather colour and weather during moult

Year	ASY male	ASY female	SY male	SY female
2001	2	0	10	0
2002	16	0	24	0
2003	18	3	13	1
2004	27	21	23	15
2005	43	13	37	12
2006	38	10	14	17
2007	44	15	10	11
2008	22	1	16	0
2009	25	12	15	9
2010	19	0	13	0
2011	7	1	1	0

Colour analysis

Plumage colouration was quantified by reflectance spectrometry using an Ocean Optics JAZ spectrometer with a xenon light source and measuring reflectance across the avian visual range (300–700 nm). Prior to colour analysis, all feathers were mounted on low reflectivity (<5 %) black paper (Colorline Ebony #142). Ten measurements from each feather were taken haphazardly within the orange/yellow region of the feather, not including the rachis, with the probe held within a non-reflective sheath 5.9 mm from the feather at a 90° angle. Measurements were standardized between each successive feather using an Ocean Optics WS-1 white standard and non-reflective dark standard.

Reflectance measurements were analysed in the R-based colour analysis program RCLR v.28 (Montgomerie 2008). Prior to calculating colour variables, we performed a smoothing function on all curves to eliminate noise and local peaks. We then calculated brightness, red chroma, and hue. Brightness was calculated as the mean amount of light reflected across the visual spectrum mean ($R_{300-700}$), while red chroma was calculated as $(R_{605-700}/R_{300-700})$. Hue was calculated via segment classification ($\arctan\{[(R_{415-510} - R_{320-415})/R_{320-700}]/[(R_{575-700} - R_{415-575})/R_{320-700}]\}$), and provides information on the dominant wavelength of light reflected. Both chroma and hue are generally considered good indicators of carotenoid content (Saks et al. 2003). Low values indicate feathers shifted towards longer orange/red wavelengths, while higher values indicate feathers shifted towards shorter, yellow, wavelengths. The 10 measurements for each individual feather were then averaged to produce a single brightness, red chroma, and hue value for each feather. Colour analysis methods and calculations follow previous work by our group on American redstarts (e.g., Reudink et al. 2009a, b; Tonra et al. 2014).

Table 2 Summary of the top-ranked models (<4 AICc units from top model) explaining variation in feather brightness, red chroma, and hue for ASY and SY American redstarts (model details at table bottom)

Model category	Top models	AICc	Δ AICc	w_i
ASY brightness				
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Rn	-1,089.9	0.00	0.31
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Tp	-1,089.6	0.31	0.26
	Sex + Jn.Rn + Jl.Tp + sex \times Jl.Rn + sex \times Jl.Tp	-1,088.9	1.00	0.19
	Sex + Jl.Rn + sex \times Jl.Rn	-1,088.4	1.52	0.14
SY brightness				
	Sex + Jl.Rn + Jl.Tp	-645.8	0.00	0.33
	Sex + Jl.Rn	-645.3	1.54	0.25
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Tp	-643.9	1.90	0.13
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Rn	-643.8	2.03	0.12
	Sex + Jl.Rn + sex \times Jl.Rn	-643.2	2.64	0.09
ASY red chroma				
	Sex + Jl.Rn + sex \times Jl.Rn	-1,610.2	0.00	0.31
	Sex + A.Tp ^d + sex \times A.Tp	-1,608.7	1.46	0.15
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Rn	-1,608.1	2.10	0.11
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Tp	-1,608.0	2.19	0.10
	Sex + A.Rn + A.Tp + sex \times A.Tp	-1,607.1	3.03	0.07
	Sex + Jl.Rn	-1,607.0	3.19	0.06
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Rn + sex \times Jl.Tp	-1,606.8	3.41	0.06
SY red chroma				
	Sex + Jl.Rn	-1,298.6	0.00	0.40
	Sex + Jl.Rn + Jl.Tp	-1,296.6	1.98	0.15
	Sex + Jl.Rn + sex \times Jl.Rn	-1,296.5	2.10	0.14
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Tp	-1,296.2	2.35	0.12
	Sex + Jl.Rn + Jl.Tp + sex \times Jl.Rn + sex \times Jl.Tp	-1,295.3	3.24	0.08
ASY hue				
	Sex + A.Tp + sex \times A.Tp	-405.6	0.00	0.28
	Sex + A.Rn + A.Tp + sex \times A.Rn + sex \times A.Tp	-404.1	1.44	0.13
	Sex + A.Rn + A.Tp + sex \times A.Tp	-404.0	1.57	0.13
	Sex + Jl.Rn + Jl.Tp	-401.9	3.61	0.05
	Sex	-401.7	3.90	0.04
SY hue				
	Sex + A.Rn + A.Tp + sex \times A.Tp	-115.2	0.00	0.11
	Sex + S.Tp + sex \times S.Tp	-114.8	0.41	0.09
	Sex + A.Rn + A.Tp	-114.7	0.55	0.09
	Sex + A.Rn	-114.4	0.78	0.08
	Sex + A.Tp + sex \times A.Tp	-114.1	1.09	0.07
	Sex + S.Tp	-114.0	1.28	0.06
	Null model	-113.7	1.57	0.05

The AICc value, difference in AICc between the model and the top model (Δ AICc), and model weights (w_i) are shown. Year and individual were included as random effects in all ASY models, and year was included as a random effect in all SY models. Note that only the top 7 models are shown for SY hue (18 models were within 4 AICc units)

J June, Jl July, A August, S September, Rn total rainfall, Tp mean temperature (e.g., Jl.Tp = mean July temperature)

Weather data

We obtained rainfall and temperature information for the Ontario breeding grounds from a weather station at QUBS. We used monthly total rainfall and mean air temperature from June–September as proxies for breeding season weather in year_{*x*-1}, to be related to feather colour in year_{*x*} (see “[Statistical analyses](#)”). Thus, we obtained weather data for the years 2000–2010 in order to relate them to feather colour in the years 2001–2011. However, QUBS weather

data were not available for 2010, and so instead we used temperature and rainfall data from a nearby Environment Canada weather station (Ottawa, Ontario, approximately 100 km to the northeast of our study site). Weather data from the QUBS and Environment Canada stations were generally highly correlated for 2000–2009 (see below), and so we felt justified using Environment Canada data for 2010. Nonetheless, if weather data from 2010 (and feathers from 2011) were excluded, our results remained unchanged (note small sample size of feathers for 2011 compared to

other years; Table 1). We also compared our weather data to datasets from an additional two nearby weather stations—Kingston, Ontario (approximately 40 km south and available for 2000–2006), and Toronto, Ontario (approximately 260 km southwest and available for 2000–2010). When comparing all three Environment Canada stations to data from QUBS, we found temperature data to be very highly correlated (all $r > 0.92$). Correlations for rainfall were not as high though were generally positive (mean $r = 0.35$), likely reflecting more localized and variable levels of precipitation. In any case, we felt confident that our weather dataset was a reasonable representation of local weather from an area that would have encompassed the moulting location of many American redstarts from our study site. Indeed, the authors have often observed birds moulting in the late season (July and August) on our study site, and stable isotope analysis suggests moult during migration may be uncommon (Reudink et al. 2008).

Statistical analyses

To examine population-level variation in feather colour in association with weather, we constructed models that related feather colour variables in year_x to total monthly rainfall and mean monthly temperature for June–September in year_{x-1}.

To avoid problems of multiple correlation and because potential influences of weather variables on colour should occur within the same month, only rainfall and temperature from a given month were allowed in the same model. We included sex in all models and allowed for interactions between sex and rainfall or sex and temperature. Thus, a full model for the month of June would include sex, total rainfall in June, mean temperature in June, sex \times total rainfall in June, and sex \times mean temperature in June. The total set of models we evaluated included all combinations of the previous variables (with the requirement that sex be included), for each of 4 months, for a total of 34 models, including a null model and a sex-only model. We analysed the three colour variables (brightness, red chroma, and hue) separately and analysed ASY and SY birds separately, since adults and juveniles are predicted to grow their feathers during different time periods. Year was included as a random effect in all models, and individual was included as a random effect in all ASY models. We standardized temperature and rainfall data prior to analysis by subtracting values by the mean and dividing by the standard deviation so that main effects would remain biologically interpretable when involved in interactions and coefficients would be comparable in magnitude (Schielzeth 2010). We ranked models with Akaike's information criterion corrected for small sample size (AICc) and considered models within 4 AICc units to be competitive (Burnham and Anderson

Table 3 Model-averaged parameter estimates and 95 % CI for variables included in the top-ranked models (≤ 4 AICc units of best model) explaining variation in feather brightness, red chroma, and hue for ASY and SY American redstarts

	ASY brightness	SY brightness	ASY chroma	SY chroma	ASY hue	SY hue
Sex	0.0019 (–0.012, 0.016)	0.044 (0.024, 0.063)	0.011 (0.0054, 0.017)	–0.0063 (–0.011, –0.0012)	–0.24 (–0.28, –0.21)	–0.033 (–0.09, 0.23)
Jn.Tp						–0.018 (–0.12, 0.08)
Sex \times Jn.Tp						0.041 (–0.01, 0.092)
Jl.Rn	–0.0085 (–0.03, 0.012)	–0.022 (–0.035, –0.0095)	0.0035 (–0.0048, 0.0012)	0.0058 (0.0016, 0.01)	–0.082 (–0.17, 0.0058)	–0.036 (–0.12, 0.049)
Jl.Tp	–0.018 (–0.04, 0.0029)	–0.0078 (–0.02, 0.0048)	0.0036 (–0.0057, 0.013)	–0.0026 (–0.0085, 0.0033)	–0.086 (–0.17, –0.0043)	
Sex \times Jl.Rn	–0.016 (–0.032, –0.0002)	0.0022 (–0.018, 0.023)	0.0066 (0.0013, 0.013)	0.0015 (–0.0053, 0.0083)		
Sex \times Jl.Tp	0.015 (0.0029, 0.034)	–0.0047 (–0.024, 0.015)	–0.0063 (–0.014, 0.0017)	0.0044 (–0.0017, 0.01)		
A.Rn			–0.0015 (–0.0055, 0.0025)		–0.038 (–0.12, 0.043)	–0.073 (–0.15, 0.0043)
A.Tp			–0.002 (–0.0088, 0.0047)		0.013 (–0.09, 0.12)	0.046 (–0.044, 0.13)
Sex \times A.Rn					0.022 (–0.0068, 0.051)	0.0085 (–0.047, 0.064)
Sex \times A.Tp					0.045 (0.011, 0.079)	0.044 (–0.0088, 0.097)
S.Rn			–0.0066 (–0.012, –0.00076)			0.034 (–0.058, 0.13)
S.Tp						0.045 (–0.047, 0.14)
Sex \times S.Rn						–0.037 (–0.1, 0.025)
Sex \times S.Tp						0.05 (–0.01, 0.12)

Values in bold indicate that the 95 % CI did not overlap zero. See Table 2 for variable abbreviations

2002). We tested models for multiple correlation and overdispersion. Standardized total rainfall and mean temperature were not strongly correlated within models (all $r < 0.02$), and we did not detect any overdispersion in our models (all $p > 0.5$). To supplement the above analyses, we used linear regression analyses weighted by sample size of feathers to examine the relationship between mean annual colour variables and those mean weather variables identified as important in model selection. Finally, to test whether the above population-level changes could be explained by change in individual feather colour, we used a subset of 42 ASY males that were present on our study site in at least 2 consecutive years. We modelled change in colour as a function of change in those weather variables deemed important in the above analyses. Individual was again included as a random effect to account for those ASY males present across >2 years. We evaluated the significance of the weather variables by removing each and comparing the difference in deviance between the resultant model and the full model. Differences in deviance approximately follow a Chi square distribution with one degree of freedom (Zuur et al. 2009). The same models could not be run for ASY females due to very small numbers of consecutively returning birds ($n = 3$). All analyses were performed in R v.3.0.1 (R Development Core Team 2013).

Results

Brightness

The top model explaining variation in ASY feather brightness in year_x included effects of sex, July rainfall in year_{x-1}, July temperature in year_{x-1}, and the interaction between sex and July rainfall in year_{x-1} (Table 2). Other models within 4 AICc units included the above effects in addition to June rainfall and the interaction between sex and July temperature. These results indicate that July weather appeared to have a stronger association with feather brightness in comparison to weather from other months and that ASY males and females may have responded differently to July weather. Specifically, confidence intervals for model-averaged parameter estimates for the interaction between sex and July rainfall did not overlap zero (Table 3) and indicated that lower July rainfall was associated with brighter feathers more strongly in males (i.e., steeper slopes) than in females (Fig. 1a). Across years, lower July rainfall in year_{x-1} was associated with brighter feathers in ASY males in year_x, and no other relationships were significant (rainfall: males $R^2 = 0.49$, $t_9 = -2.96$, $p = 0.016$, females $R^2 = 0.09$, $t_6 = 0.77$, $p = 0.470$; temperature: males $R^2 = 0.00$, $t_9 = -0.13$, $p = 0.900$, females $R^2 = 0.35$, $t_6 = -1.81$, $p = 0.121$; Fig. 2). Based on the

above results we examined the relationship between individual change in ASY male feather brightness and annual change in July rainfall, which revealed a significant effect of July rainfall ($\chi^2_1 = 8.79$, $p = 0.003$).

The top model explaining variation in SY feather brightness in year_x included effects of sex, July rainfall, and July temperature in year_{x-1}. Other competitive models included interactions between sex and July rainfall or temperature (Table 2). Model-averaged parameter estimates indicated that SY males had brighter feathers than SY females and that lower July rainfall was associated with brighter feathers (Table 3). Across years, lower July rainfall in year_{x-1} was associated with brighter feathers in SY males in year_x, and no other relationships were significant (Rainfall: males $R^2 = 0.70$, $t_9 = -4.54$, $p = 0.001$, females $R^2 = 0.42$, $t_4 = -1.72$, $p = 0.161$; temperature: males $R^2 = 0.00$, $t_9 = -0.07$, $p = 0.949$, females $R^2 = 0.08$, $t_4 = 0.59$, $p = 0.585$; Fig. 3).

Red chroma

The top model explaining variation in ASY feather red chroma included effects of sex, July rainfall in year_{x-1}, and their interaction. Other competitive models included July temperature and its interaction with sex, as well as August temperature, August rainfall, and the interaction between sex and August temperature (Table 2). Model-averaged parameter estimates indicated that male feathers had higher red chroma than female feathers, and that male feather chroma may have been more strongly associated with weather than female feather chroma (Table 3). Specifically, ASY male chroma appeared to be more strongly reduced following years of low July rainfall and years of high August temperature in comparison to females (Fig. 1b, c). Across years, higher July rainfall in year_{x-1} was associated with higher red chroma in feathers of ASY males in year_x, and no other relationships were significant (rainfall: males $R^2 = 0.54$, $t_9 = 3.24$, $p = 0.010$, females $R^2 = 0.00$, $t_6 = 0.09$, $p = 0.934$; temperature: males $R^2 = 0.16$, $t_9 = -1.30$, $p = 0.226$, females $R^2 = 0.01$, $t_6 = -0.24$, $p = 0.820$; Fig. 4a–d). Similarly, lower temperature in August in year_{x-1} was associated with higher red chroma in feathers of ASY males in year_x, and no other relationships were significant (rainfall: males $R^2 = 0.00$, $t_9 = -0.18$, $p = 0.864$, females $R^2 = 0.28$, $t_6 = -1.51$, $p = 0.182$; temperature: males $R^2 = 0.50$, $t_9 = -3.02$, $p = 0.015$, females $R^2 = 0.29$, $t_6 = -1.56$, $p = 0.169$; Fig. 4e–h). Based on the above results, we examined relationships between both July rainfall and August temperature and individual change in ASY male feather chroma. We found that individual change was significantly predicted by August temperature ($\chi^2_1 = 11.42$, $p < 0.001$), but not by July rainfall ($\chi^2_1 = 1.68$, $p = 0.194$).

Fig. 1 Interaction effects from models explaining variation in ASY American redstart (*Setophaga ruticilla*) feather colour. **a** Feather brightness and July rainfall, **b** red chroma and July rainfall, **c** red chroma and August temperature, and **d** hue and August temperature. Shown is the mean feather colour variable in year_x in years of high (those above and including the median) or low (those below the median) rainfall or temperature in year_{x-1}. *Solid line* males, *dashed line* females

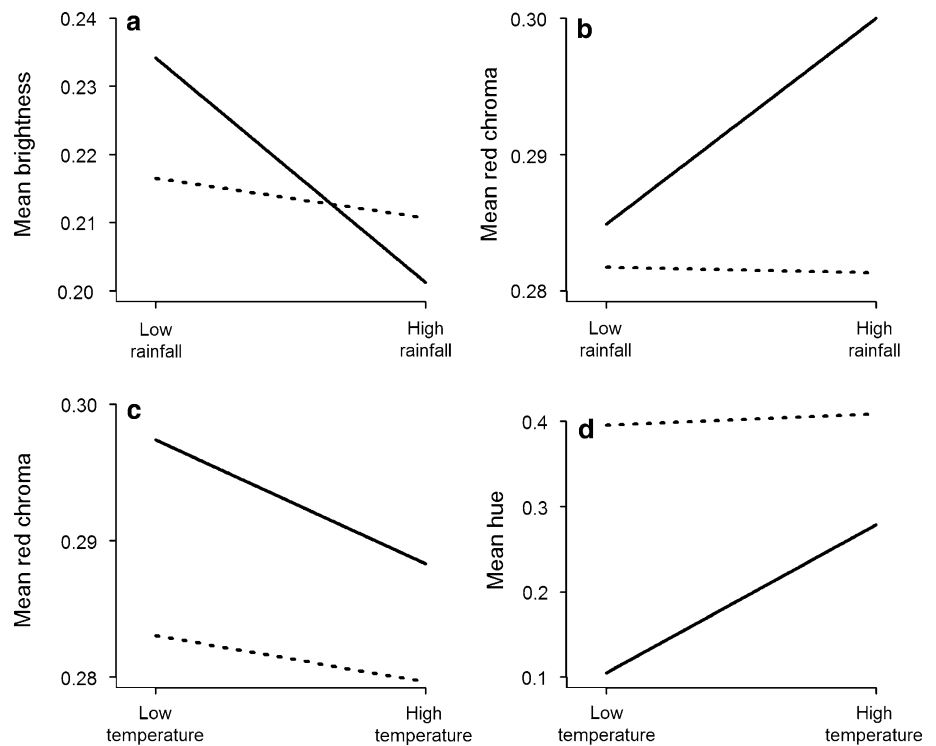
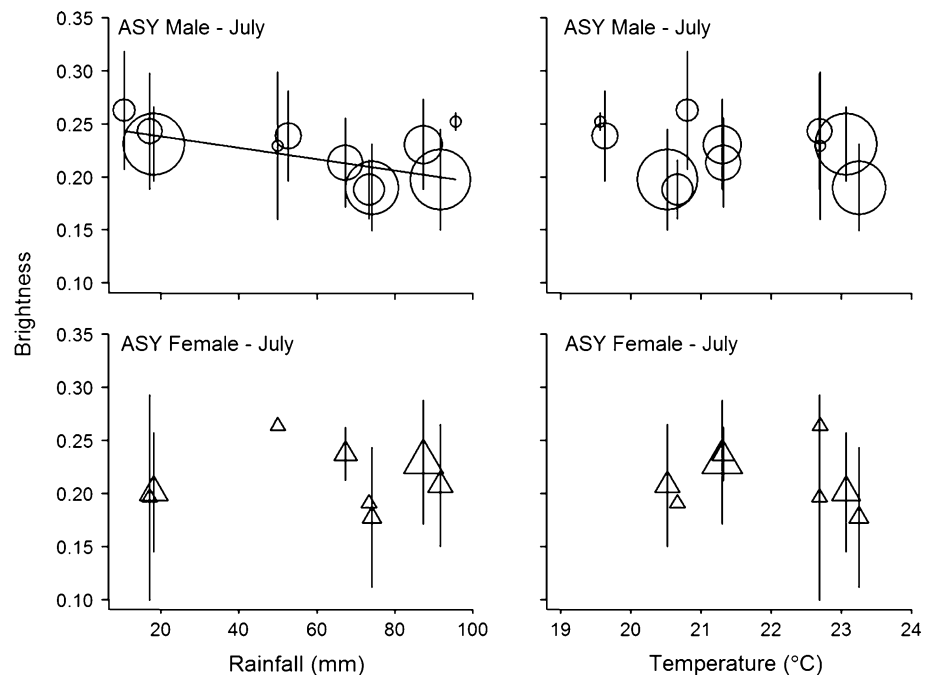


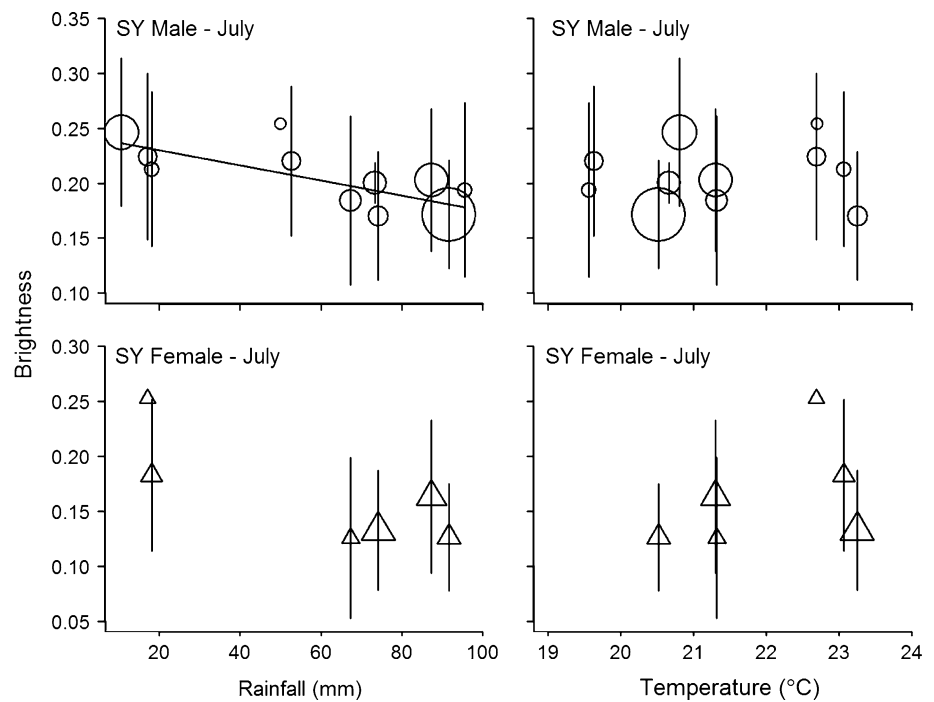
Fig. 2 Relationship between mean annual feather brightness (\pm SD) and July weather for ASY male and female feathers. Data points are weighted by sample size, and *solid line* shows a significant relationship



Results for SY red chroma showed some similarities to those for ASY birds, with sex and July rainfall included in the top model and other competitive models including July temperature and interactions between sex and July temperature or sex and July rainfall (Table 2). Model-averaged parameter estimates indicated that higher July rainfall was associated with higher red chroma, and male feathers had

higher red chroma than female feathers (Table 3). In contrast to ASY birds, no significant interactions were found between sex and weather (Table 3). Across years, higher July rainfall in year_{x-1} was associated with higher values of red chroma in SY male feathers in year_x, and all other relationships between red chroma and July rainfall or temperature across years were non-significant (rainfall:

Fig. 3 Relationship between mean annual feather brightness (\pm SD) and July weather for SY male and female feathers. Data points are weighted by sample size, and *solid line* shows a significant relationship



males $R^2 = 0.75$, $t_9 = 5.22$, $p < 0.001$, females $R^2 = 0.32$, $t_4 = 1.36$, $p = 0.244$; temperature: males $R^2 = 0.07$, $t_9 = -0.84$, $p = 0.422$, females $R^2 = 0.43$, $t_4 = -1.72$, $p = 0.161$; Fig. 5).

Hue

The top model explaining variation in ASY feather hue included effects of sex, August temperature in year_{x-1}, and their interaction. Other competitive models included August rainfall and its interaction with sex, as well as July rainfall and July temperature (Table 2). Model-averaged parameter estimates indicated that ASY male feathers had lower hue values compared to ASY female feathers and appeared to respond more strongly to August temperature, with higher hue following years of higher temperature (Table 3; Fig. 1d). In contrast, higher July temperature was associated with lower hue. No clear patterns were evident across yearly means for July weather and ASY feather hue (rainfall: males $R^2 = 0.08$, $t_9 = -0.88$, $p = 0.401$, females $R^2 = 0.04$, $t_6 = 0.47$, $p = 0.653$; temperature: males $R^2 = 0.08$, $t_9 = -0.89$, $p = 0.397$, females $R^2 = 0.30$, $t_6 = -1.62$, $p = 0.156$; Fig. 6a–d) or August weather and ASY feather hue (rainfall: males $R^2 = 0.00$, $t_9 = -0.09$, $p = 0.934$, females $R^2 = 0.01$, $t_6 = 0.25$, $p = 0.813$; temperature: males $R^2 = 0.13$, $t_9 = 1.16$, $p = 0.275$, females $R^2 = 0.05$, $t_6 = -0.59$, $p = 0.579$; Fig. 6e–h). Based on the above results, we examined relationships between both July temperature and August temperature and individual change in ASY male feather hue. We found that individual

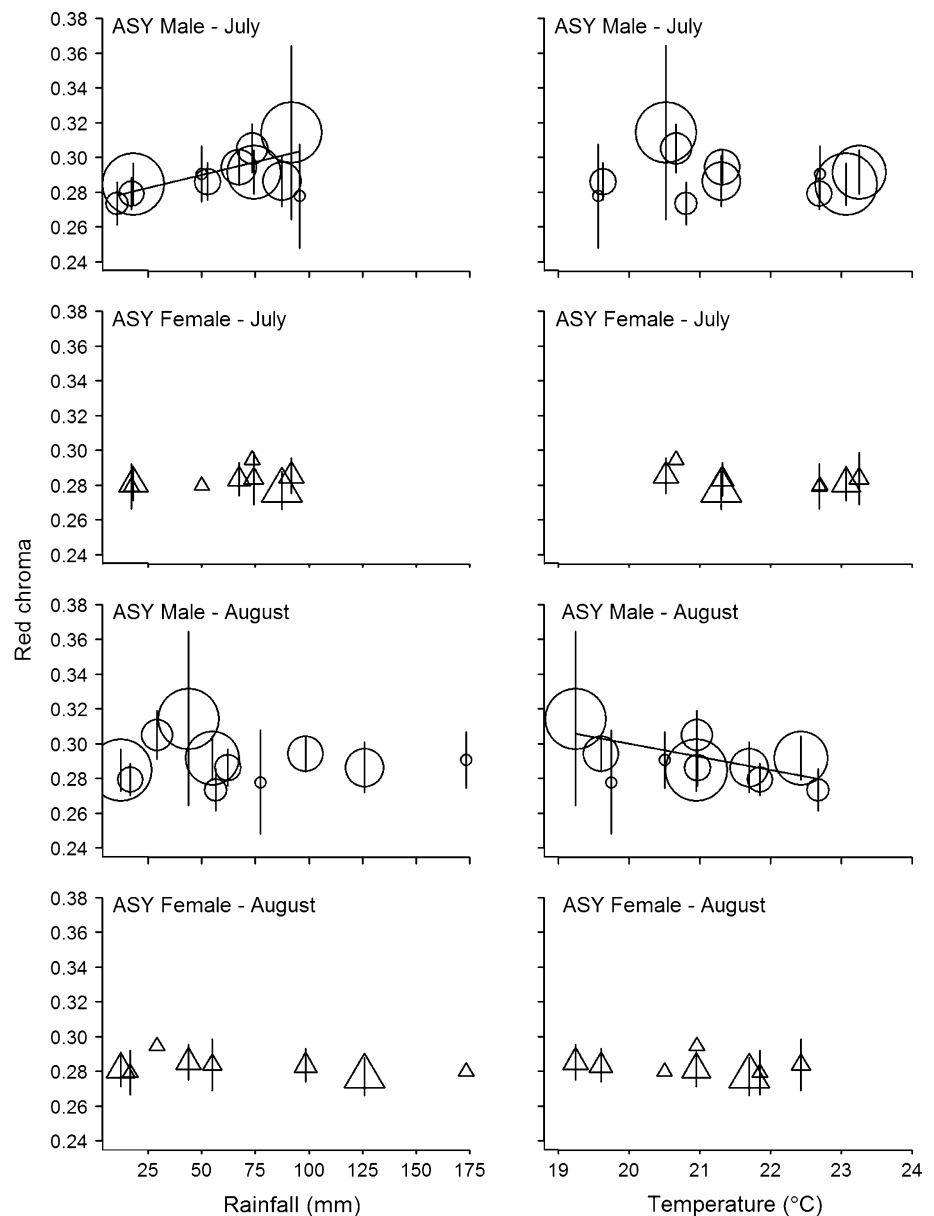
change was significantly predicted by August temperature ($\chi^2_1 = 4.40$, $p = 0.040$), but not by July temperature ($\chi^2_1 = 2.54$, $p = 0.111$).

Compared to feather brightness and red chroma, SY feather hue appeared to be less influenced by weather. Eighteen models were competitive with the top-ranked model explaining variation in feather hue, indicating that many different models were equally likely given the data, and this set also included the null model (Table 2). We did not make annual comparisons for SY birds due to no clear weather variables appearing important in influencing individual variation in feather hue.

Discussion

Environmental factors, such as temperature and rainfall, can have major impacts on migratory birds at both the individual and population level. High primary productivity associated with increased rainfall on the wintering grounds may result in high over-winter survival, which is reflected in high breeding season abundance (Wilson et al. 2011). Similarly, productivity on the breeding grounds can be strongly affected by climatic conditions (reviewed in Newton 1998), with variation in temperature and rainfall influencing the timing of breeding (Dunn 2004) and arrival (McKellar et al. 2013), productivity (Wilson and Arcese 2004) and survival due to changes in food abundance (Morrison and Bolger 2002; Collister and Wilson 2007). These pathways can also be influenced by local climate

Fig. 4 Relationship between mean annual feather red chroma (\pm SD) and July and August weather for ASY male and female feathers. Data points are weighted by sample size, and *solid lines* show significant relationships

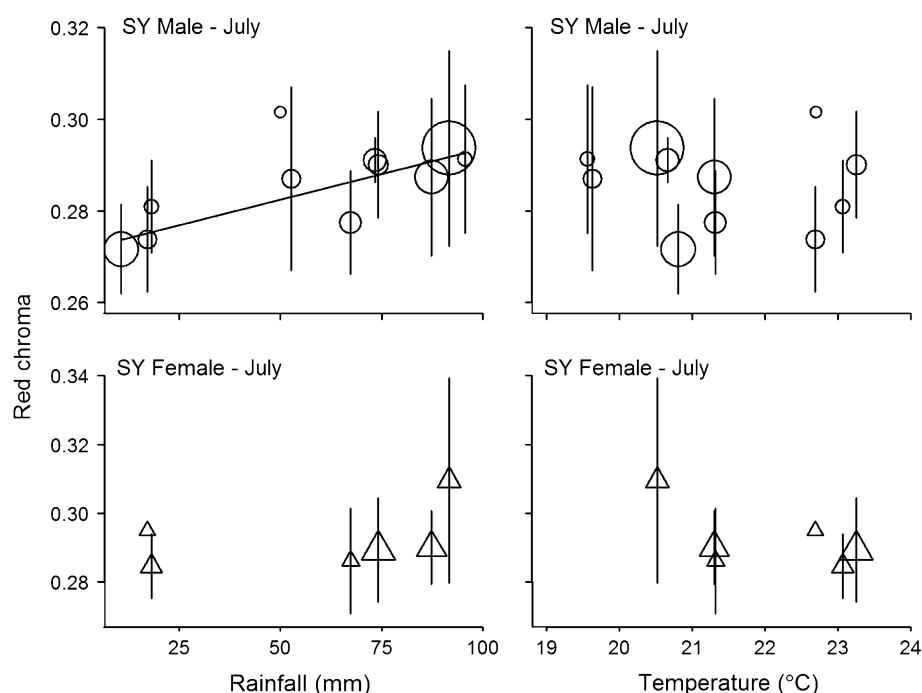


conditions en route (Tøttrup et al. 2008). In this study, we demonstrate that weather conditions later in the breeding season may also have important effects on plumage colouration. American redstarts showed associations between the brightness, red chroma and, to a lesser extent, hue of their tail feathers in relation to breeding season weather conditions the previous year. In general, individuals expressed plumage with higher red chroma (Figs. 4, 5), lower brightness (Figs. 2, 3), and more orange-shifted hue (Fig. 6) in years following high July rainfall or temperature and lower August temperature.

In our population of American redstarts, individuals begin breeding in mid- to late May, and by July have either completed breeding attempts (due to not successfully pairing or raising offspring) or are in the latter stages of raising

nestlings or fledglings. By late July, many individuals have begun the process of moult prior to fall migration, sometimes overlapping moult and nestling provisioning in late nests (unpublished data). During this time, rainfall can be especially variable, with July total rainfall ranging from 11 to 96 mm over 11 years. Across certain age and sex classes, rainfall and temperature during moult appeared to predict plumage colouration the subsequent season. We suggest that the most likely mechanism for this pattern is differences in insect abundance, with higher insect abundance resulting from high levels of rainfall (e.g., Moser 1967; Boomsma and Leusink 1981). For example, work on great tits demonstrated that the proportion of leaf-eating insects (primarily carotenoid-rich Lepidoptera larvae) in the diet of nestlings declined drastically over the breeding season;

Fig. 5 Relationship between mean annual feather red chroma (\pm SD) and July weather SY male and female feathers. Data points are weighted by sample size, and *solid line* shows a significant relationship



correspondingly, carotenoid content was significantly higher in first-brood nestlings than in later nestlings (Ilyina et al. 2013). Similarly, Eeva et al. (2005, 2008) demonstrated that nestling great tits inhabiting regions with high levels of industrial pollution and fewer Lepidopteran larvae grew less intensely coloured yellow ventral feathers.

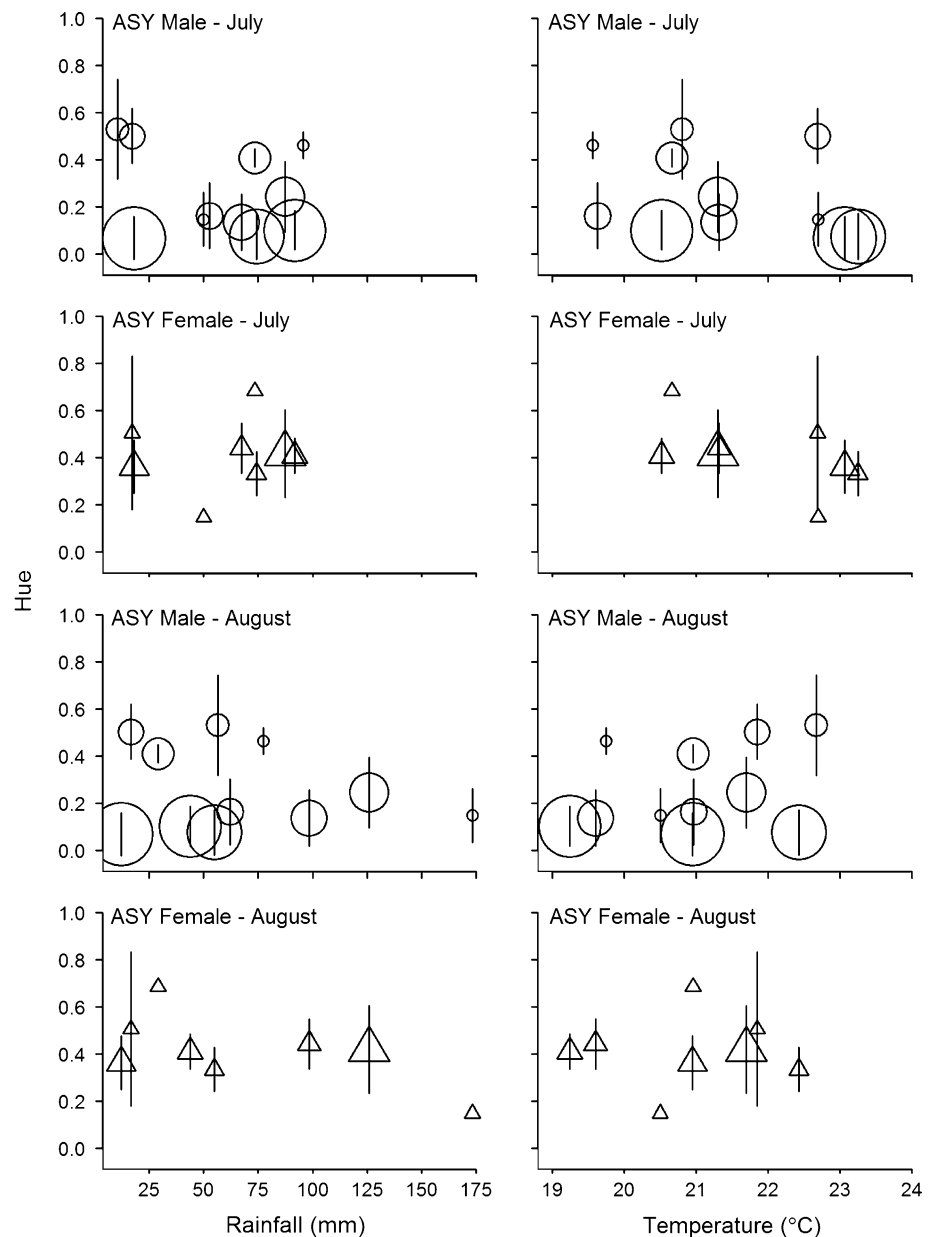
These findings parallel a substantial body of work in the American redstart showing the influence of rainfall during the wintering period on insect abundance and subsequent body condition (Studds and Marra 2007; Angelier et al. 2011), migratory timing (Studds and Marra 2011; McKellar et al. 2013), and abundance (Wilson et al. 2011). However, we are not aware of other studies that have shown weather-associated changes in feather colouration during moult, although long-term changes in climatic conditions have been linked to population-level changes in colouration in some species. Melanin-based plumage redness in scops owls (*Otus scops*) has increased significantly over the past century—a period associated with increases in temperature and rainfall (Galeotti et al. 2009). Globally, a similar pattern was observed across four owl genera [wood (*Strix*), scops (*Otus*), screech (*Megascops*), and pygmy owls (*Glauucidium*)], with darker red phenotypes observed in lower latitudes with warmer climates (Roulin et al. 2011).

American redstarts prey on a variety of insects including Lepidoptera larvae, which are highly concentrated in carotenoid pigments (Eeva et al. 2010) and are one of the major food sources during the breeding season (Sherry and Holmes 1997). High July rainfall likely results in increased insect availability, which may increase individual condition and also increase dietary carotenoid availability. We

suggest that redstart feather colouration varies at an individual and a population level due to annual variation in the availability of insects and dietary carotenoids, as increased rainfall was positively associated with increased red chroma and reduced brightness in ASY males, which may positively reflect carotenoid content (Saks et al. 2003). Perhaps most importantly, the patterns that we observed were consistent across age classes, though patterns were stronger in males than in females (Table 2; Fig. 1), suggesting that environmental effects, rather than solely individual-level trade-offs (e.g., trade-offs with reproductive effort; Sieferman and Hill 2005; Doutrelant et al. 2012), can have important influences on plumage colouration.

Plumage colouration of both ASY and SY individuals was most often associated with conditions the previous July and August, though weather from other months appeared in some top-ranked models (Table 2). Hatch-year birds (i.e., those who would be SY birds the following season) may grow their feathers in the nest as early as June, though many would certainly do so into July or even August. Adult birds typically begin moult in July, though many likely moult primarily in August and potentially into September, especially those individuals with late-season nesting attempts (see “Introduction”). Further research would be needed to identify the basis for the particular importance of rainfall in July and temperature in August over conditions in other months, perhaps as it relates to insect emergence and abundance. In contrast, we found some evidence for differential strength of effects of weather between males and females (i.e., significant interactions in Table 2 and differing slopes in Fig. 1). These relationships most often

Fig. 6 Relationship between mean annual feather hue (\pm SD) and July and August weather for ASY male and female feathers. Data points are weighted by sample size



indicated that female colouration may have responded less strongly to weather conditions than male colouration, though sample sizes were smaller for females (Table 1). Possible reasons for differences in the strength of associations between feather colouration and weather include sex-specific foraging preferences or differences in moult patterns, in addition to obvious differences in feather carotenoid content between males and females. Additionally, differences in selective pressures for signalling exerted on males and females could result in a differential response to weather conditions during moult.

In American redstarts, variation in plumage colouration is strongly associated with variation in reproductive success on the breeding grounds (Reudink et al. 2009a), as well as

winter territory quality on their tropical wintering grounds (Reudink et al. 2009b). Our findings of individual change in feather colouration in association with environmental conditions during moult raise interesting questions about the relative importance of environmental and genetic effects (e.g., genotype-by-environment interactions; Qvarnstrom 1999; Roulin et al. 1998, 2008) and the condition-dependence of signalling traits (Cotton et al. 2004). For example, male American redstart (both SY and ASY) with brighter tail colouration are more likely to occupy dominance-mediated high-quality winter habitats in Jamaica, suggesting that tail brightness may be acting as an intra-sexual signal (Reudink et al. 2009b). Because birds wintering in the Caribbean breed across a broad range of latitudes in eastern North

America (Norris et al. 2007), variation in environmental conditions and their interaction with intrinsic factors could influence the reliability of tail colouration as an honest signal of individual quality on the wintering grounds.

In conclusion, we demonstrate that, over an 11-year period, American redstarts exhibited substantial inter-year variation in plumage colouration that appeared to be associated with weather conditions during moult, perhaps due to increased dietary availability of carotenoids following higher insect abundance. While many studies have examined the influence of climate on population dynamics (e.g., survival, productivity), very few have examined the influence of environmental conditions on the expression of sexually selected traits. This work demonstrates a potentially critical seasonal interaction, whereby weather conditions during post-breeding moult may carry over to impact intersexual signalling during the non-breeding season and the intensity of sexual selection during the subsequent breeding season. Future studies into environmentally-induced variation in sexual signals and their effects on sexual selection, mate choice, and the reliability of putative signals may reveal how these pressures could shift with a changing global climate (e.g., Cockburn et al. 2008).

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