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Plumage coloration predicts paternity and polygyny in the American redstart

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Many animals display multiple signals that can be used by conspecifics to gather information about the condition or quality of potential mates or competitors. Different signals can indicate different aspects of individual quality or function in spatially or temporally separated periods. However, for long-distance migratory birds, it is unclear if signals, such as plumage traits, function in different phases of the annual cycle. We investigated the potential role of carotenoid-based tail and flank plumage, and bib size, in relation to extrapair paternity and polygyny in the American redstart, *Setophaga ruticilla*. This work complements our previous research suggesting tail feather brightness acts as a status signal, mediating territory acquisition during the nonbreeding season in Jamaica. Here, we show that tail feather brightness also serves as an important signal during the breeding season. Specifically, our results indicate that polygyny, a behaviour highly dependent on obtaining and defending multiple territories, is significantly predicted by tail brightness. Interestingly, flank redness best predicted whether individuals secured paternity at their nest and the proportion of within-pair offspring sired. We suggest that by expanding the study of plumage function in long-distance migrants to events occurring throughout the annual cycle, we gain a critical perspective on the function and evolution of ornamental traits.

Sexual dimorphism and the widespread occurrence of exaggerated ornamental traits in animals are generally attributed to evolution through sexual selection, where more ornamented males obtain a disproportionate share of matings (Andersson 1994). If these traits are costly to produce, they can thus act as honest signals of individual quality (Kodric-Brown & Brown 1984). Many species have more than one trait that may convey information, such as vocalizations, behavioural displays, and plumage or multiple plumage characters (Andersson 1994). The presence of multiple ornaments is perplexing, and a number of theories have been put forth to explain their evolution. Multiple ornaments could evolve under arbitrary Fisherian selection (Fisher 1958; Kirkpatrick 1982; Møller & Pomiankowski 1993), selection for a single most-revealing trait (Schluter & Price 1993; Iwasa & Pomiankowski 1994), or selection for multiple quality-revealing traits (Johnstone 1995; Doucet & Montgomerie 2003; Papke et al. 2007; Taylor et al. 2007). Preference for male traits can also vary based on plasticity in female choice under differing demographic conditions or female reproductive states (Uetz & Norton 2007) or preference for different traits in different years (Chaine & Lyon 2008).

Furthermore, multiple signals may be intended for different receivers (Pryke et al. 2001; Andersson et al. 2002; Pryke et al. 2002; Braune et al. 2005), indicate different aspects of individual quality (Doucet & Montgomerie 2003; Jawor & Breitwisch 2004), or function in spatially or temporally separated periods (Marchetti 1998; Braune et al. 2005). For example, red-collared widowbirds, *Euplectes ardens*, have an elongated tail and a red, carotenoid-based collar. Both tail length and carotenoid coloration are classic examples of sexually selected traits; however, only elongated tail length is preferred by females and associated with mating success (Pryke et al. 2001). The red collar, on the other hand, appears to function in agonistic, intrasexual interactions (Pryke et al. 2002). Such studies highlight the need to investigate the function of multiple ornaments throughout the annual cycle, both in the context of sexual signalling during the breeding season as well as agonistic signalling during the nonbreeding period. For migratory birds, elucidating the function of plumage-based signals throughout the annual cycle can be particularly onerous, as some signals may function during migration or on the wintering grounds, thousands of kilometres removed from the breeding grounds. In particular, plumage may act to mediate access to food resources at migratory stopover sites (Moore & Yong 1991), or territory acquisition (Reudink et al., in press) and agonistic interactions during the nonbreeding season (Rohwer 1975).

American redstarts, *Setophaga ruticilla*, provide a unique opportunity to study the function of multiple plumage traits on both the breeding and wintering grounds. Plumage in after-second-year

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(ASY) male redstarts is highly variable in both carotenoid-based (orange) regions and in the size of the melanin-based (black) bib, making this an ideal species for the study of the relative importance of multiple potential signals. Both carotenoid- and melanin-based plumage traits may reveal individual quality, although the mechanisms that maintain signal honesty can vary between pigment types. Carotenoid-based pigments cannot be synthesized naturally by birds and must be ingested as part of the diet. Thus, only males that are in good condition and that can secure access to high-quality food sources should be able to acquire high-quality plumage (Hill 1992, 1999; Hill & Montgomerie 1994; Brawner et al. 2000). Carotenoid-based plumage is a reliable sexual signal in a number of passerines (reviewed in: Griffith & Pryke 2006; Hill 2006). Unlike carotenoids, melanin is synthesized from naturally occurring amino acids, but signal honesty can be maintained through social reinforcement mechanisms (Senar 2006) or nutrient limitation (McGraw 2007). Melanin-based signals, especially badge size, can signal status in temperate resident species during the nonbreeding season (Rohwer 1975; Fugle et al. 1984; Grasso et al. 1996; Woodcock et al. 2005), but can also act as a sexual signal during the breeding season (Møller 1988, 1990; Thusius et al. 2001; Jawor & Breitwisch 2003; Tarof et al. 2005).

American redstarts undergo a single prebasic moult at the end of the breeding season and retain those feathers throughout the winter and subsequent breeding season (Sherry & Holmes 1997). They are sexually dimorphic and males have delayed plumage maturation; females and males in their first breeding season (second year, or SY males) are grey with yellow patches on their tails, wings and flanks, while ASY males are jet black with orange patches (Sherry & Holmes 1997). SY males have severely reduced reproductive success (see below), suggesting that, at least on a gross level, plumage coloration is associated with gaining reproductive opportunities. American redstarts have a mixed mating strategy, with moderate levels of polygyny (25% of ASY males; M. W. Reudink, P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin & L. M. Ratcliffe, unpublished data) and high levels of extrapair paternity (59% of nests, 40% of offspring: Perreault et al. 1997; 43% of nests, 25% of offspring: Reudink et al., unpublished data).

Polygyny and extrapair paternity require different strategies to maximize success. Because redstart extrapair sires provide no parental investment, female mate choice for extrapair sires should be based on signals that convey genetic quality (Griffith et al. 2002). Polygynous males are polyterritorial, holding territories separated by up to 300 m. Polygyny requires defending multiple territories throughout the breeding season (Secunda & Sherry 1991), suggesting that male–male interactions may be critical in achieving polygyny. After hatching, redstart males provide parental care at both nests, although the amount of care provided at the secondary nest is reduced relative to the primary nest (Secunda & Sherry 1991; R. Germain, unpublished data). While tertiary females have been reported (Secunda & Sherry 1991), we have not recorded any incidences of males pairing with more than two females in our study population.

To the best of our knowledge, no work has yet addressed the function of plumage traits during both the breeding and nonbreeding period in a long-distance migratory songbird. However, our previous work conducted in Jamaica showed that male redstarts occupying territories in high-quality habitats during the nonbreeding season have brighter tail feathers, suggesting that tail brightness functions as a signal of competitive ability during the nonbreeding season (Reudink et al., in press). By investigating how tail feather brightness and other plumage traits are related to breeding events, we expand upon our previous work to examine whether these plumage traits function during the breeding and nonbreeding periods and/or whether different traits signal different aspects of male quality.

To investigate the potential role of tail feather coloration as a multiple-use signal, and to investigate a role for flank feather coloration and bib size, we examined the relationship between these plumage characters and extrapair paternity, polygyny and total genetic fledging success. Because the tail feathers of male redstarts are associated with winter territory acquisition, we predicted that males with brighter tail feathers would be more successful at polygyny and polyterritoriality (Secunda & Sherry 1991). We then compared the plumage characteristics of males that sired all their own offspring versus those that lost paternity at their nest. Next, we compared the characteristics of the male that lost paternity to those of the extrapair sire(s). Finally, we examined the plumage correlates of male genetic fledging success.

METHODS

Field Data Collection

Field work was conducted May–July 2005–2007 at the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44°34′N, 76°19′W). Our study area was composed of mixed-deciduous forest, primarily dominated by sugar maple (*Acer saccharum*) and eastern hophornbeam (*Ostrya virginiana*). When males arrive on the breeding grounds, they immediately begin singing for territory advertisement and to attract females. During 1–31 May, we surveyed our 60 ha study area from 0600 to 1200 hours, detecting males by the presence of singing and subsequent visual identification. ASY males arrive first on the breeding grounds (mean $\pm$ SE = May 4 ± 1.4 days), followed by females (May 9 ± 1.7 days), then SY males (May 13 ± 2.8 days). Most ASY males were captured in mist nets within 7 days of arrival by simulating territorial intrusions using song playbacks (recorded at Hubbard Brook, NH, U.S.A.) accompanied with either a stuffed ASY male decoy or a caged live male (SY or ASY). Male redstarts at our study site are extremely aggressive and relatively easy to catch. Because we monitored the entire study site on a daily basis, we were able to ensure that we captured all males holding territories within the study area. Females were captured either by simulating territorial intrusions or by using song playback of fledgling alarm calls accompanied by a female decoy. Redstarts were individually marked with a single Canadian Wildlife Service aluminium band and two to three colour leg bands. We then extracted 50 μl of blood for paternity analysis by piercing the brachial vein. Consistent with our previous work, we used wing length (mm) as our measure for relative body size (Reudink et al., in press). From each individual, we plucked a single tail feather (third rectrix, R3) and 12–15 feathers (Quesada & Senar 2006) from the center of the orange portion of the flanks. We did not pluck any primary feathers (which also have a carotenoid-based orange patch) to lessen the invasiveness of our study.

Upon arrival, all males were observed and mapped for at least 20–30 min/day to determine territory boundaries and pairing date. Females typically begin nest building within a few days of pairing. Once nest building began, we monitored nest status every other day, noting the onset of egg laying, number of eggs laid, and hatching and fledging success. Males continued to be monitored daily to ensure that we detected polygynous matings. At day 5 after hatching, we banded nestlings with a single aluminium band and took 15–20 μl of blood for paternity analysis. When nests were inaccessible, the offspring were captured on the day of fledging.

Because redstarts show delayed plumage maturation and few SY males pair and fledge offspring (one of 22 males that stayed in our study area throughout the entire season fledged a single offspring), we restricted our analyses to ASY males.

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Paternity Analysis

Blood samples taken from putative parents and offspring were stored in Queen's lysis buffer. DNA was extracted using an Invitrogen Purelink genomic DNA extraction kit (Invitrogen Corporation, Carlsbad, CA, U.S.A.). gDNA was then quantified via agarose gel electrophoresis and diluted or concentrated to ~10 ng/μl. All loci were amplified using a Biometra Thermogradient cycler or Biometra UNOII cycler PCR machine under the following conditions: 94 °C for 3 min followed by 35 cycles of 94 °C for 15 s, 58 °C for 15 s, 72 °C for 30 s, and a final extension of 72 °C for 10 min. Each sample included 1 μl of DNA (10 ng/μl), 1 μl of 10X Qiagen PCR buffer, 0.03 μl (100 mM) of dNTPs, 0.03 μl (100 μM) of forward primer, 0.03 μl (100 μM) of reverse primer, 0.025 μl of M13 F 700IRD Licor primer, 0.005 μl (5 U/μl) of Taq polymerase, and up to 10 μl total volume of sterile ddH_2O. Amplified samples were run on a Licor IR2 Global Sequencing Unity (LI-COR Biosciences, Lincoln, NE, U.S.A.), and allele scoring was conducted by a trained observer blind to the identity of individuals.

Paternity analysis was conducted using five microsatellite loci (*Dpμ*01, *Dpμ*03, *Dpμ*05, *Dpμ*15, *Dpμ*16) originally isolated from yellow warblers, *Dendroica petechia* (Dawson et al. 1997). Over the 3 years of this study, we analysed the DNA of 196 offspring (from 62 nests) and all putative parents. The use of five highly variable microsatellite loci ensured a high probability of exclusion (>0.999). Paternity exclusion and assignment was conducted using CERVUS 2.0 (Marshall et al. 1998) and double-checked by hand. Because of the limitations for detecting differences at fewer than two base pairs and the relatively high frequency of null alleles, we followed the relatively conservative approach of Reudink et al. (2006); offspring were excluded only if they mismatched the putative sire at more than two base pairs and at least at two loci. We found no evidence of maternal mismatches, suggesting there was no evidence of egg dumping and confirming that all offspring belonged to the focal nests.

Colour Variables

All feather samples were mounted on low-reflectivity black paper (<5% reflectance; Colorline no. 142 ebony, Canson Talens, Inc, South Hadley, MA, U.S.A.). The single tail feather was mounted alone, while 12–15 flank feathers were stacked as they would lie on the bird (Quesada & Senar 2006). In cases where we had an insufficient number of flank feathers or too little orange on the tail feather, that colour patch was excluded from further analyses. Percentage reflectance across the redstart's assumed visual spectrum (320–700 nm) was recorded using an Ocean Optics USB2000 spectrometer (Ocean Optics, Dunedin, FL, U.S.A.) attached to a PX-2 xenon pulsed light source (Fig. 1). The probe was held at a 90° angle from the feather surface and housed in a sheath to keep the probe a constant distance from the feather surface. Measures were standardized by taking readings from a dark (sealed, black velvet-lined box) and white (Ocean Optics WS-1) standard between each measurement. For both feather regions, we took 25 readings haphazardly throughout the region of interest. Using CLR1.0.3 (Montgomerie 2008), we gathered the raw reflectance data into 10 nm bins from 320 to 700 nm and averaged across the 25 measurements. To quantify tail and flank coloration, we first calculated brightness by averaging the percentage reflectance from 320 to 700 nm. Because redstart tail and flank feathers consist of multiple peaks (UV and red/orange), we used principal components analysis (PCA) to collapse the spectrum into a small number of independent variables that described the shape of the curve (and thus measures of hue and chroma) while controlling for variation in brightness (Cuthill et al. 1999; Grill & Rush 2000; Montgomerie 2006). To verify this method, we also calculated hue and chroma using the following calculations:

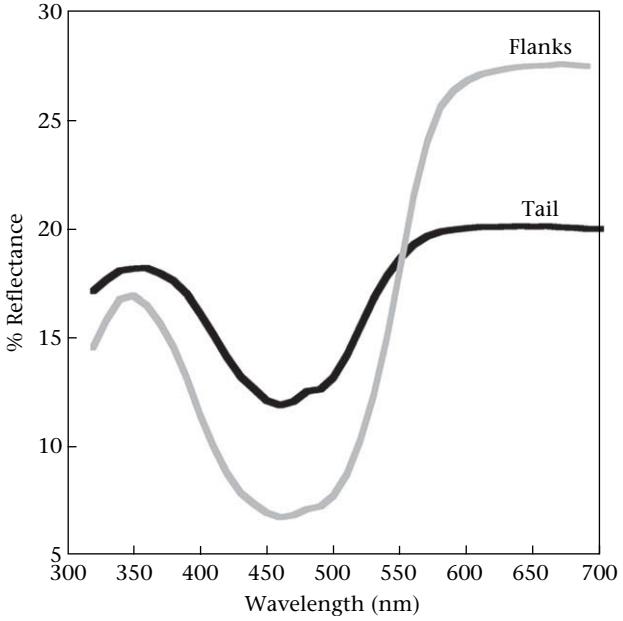

Figure 1. Average reflectance spectra of after-second-year (ASY) male flank (grey line) and tail feathers (black line).

$$\text{Hue} = \arctan((R_{\lambda 415-510} - R_{\lambda 320-415})/R_{\lambda 320-700})/((R_{\lambda 575-700} - R_{\lambda 415-575})/R_{\lambda 320-700})$$

$$\text{UV chroma} = R_{\lambda 320-415}/R_{\lambda 320-700}$$

$$\text{Red chroma} = R_{\lambda 575-700}/R_{\lambda 320-700}$$

For tail feathers, the first principal component (tail PC1) explained 67.7% of the variation in the shape of the curve and loaded positively on the shorter wavelengths and negatively on the red/orange region of the spectrum. Correspondingly, tail PC1 was negatively correlated with hue ($R^2 = 0.33$, $N = 118$, $P < 0.001$) and red chroma ($R^2 = 0.87$, $N = 118$, $P < 0.001$) and positively correlated with UV chroma ($R^2 = 0.09$, $N = 118$, $P = 0.007$). Flank PC1 described 88.9% of the variation in curve shape and, as for the tail feathers, loaded positively on the shorter wavelengths and negatively on the red/orange region of the spectrum. Again, flank PC1 was negatively correlated with hue ($R^2 = 0.81$ $N = 109$, $P < 0.001$) and red chroma ($R^2 = 0.99$, $N = 109$, $P < 0.001$) and positively correlated with UV chroma ($R^2 = 0.86$, $N = 109$, $P < 0.001$). Thus, PC1 from both tail feathers and flank feathers was used to describe 'redness', where 'redder' birds had more negative tail and flank PC1 values. Following Lemon et al. (1992), bib size was ranked in hand on ASY males on a scale from 1 to 5, where 1 = a small amount of black, 5 = a large amount of black, and intermediates are given half-points. See Lemon et al. (1992) for illustrations of bib size characteristics.

Statistical Analysis

All statistical analyses were performed in JMP 5.1 (SAS Institute 2006). For individuals that bred on the site for more than 1 year of the study, we randomly selected data only from 1 year to avoid pseudoreplication. To avoid multicollinearity among factors included in logistic regressions, we examined pairwise correlations between all predictor variables (see Results, Colour Analysis). We

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used stepwise logistic regression with presence/absence of extrapair offspring as the response variable to determine the factors that best predicted the occurrence of extrapair offspring, sequentially eliminating non-significant ($P > 0.05$) variables from the model. We also used stepwise logistic regression with polygynous/monogamous pairing as a response variable to determine the factors that best predicted whether a male achieved polygyny. To determine the factors that best predicted the proportion of within-pair offspring and total fledging success, we used backward stepwise multiple regression. We used matched-pairs t tests to compare the characteristics of extrapair and within-pair sires. Assumptions of normality were met for all parametric tests.

Ethical Note

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.

RESULTS

Paternity Analysis

Of the 44 nests from 2005 to 2007 included in this study, 22 (50%) contained one or more extrapair offspring, while 45 of the 135 (33%) offspring analysed were extrapair. Of the 22 nests that contained extrapair offspring, seven had extrapair offspring that were sired by a single male, four had offspring sired by two extrapair males, and three had offspring sired by three extrapair males. We were unable to identify extrapair sires for the remaining nests. Of the 45 extrapair offspring, we were able to assign paternity to 22. Average clutch size ±SE was 3.07 ± 0.15 (range 1–5 offspring) and contained an average of 1.02 ± 0.19 extrapair offspring (range 0–4 extrapair offspring). A subset of males for whom we collected paternity data were polygynous (10/44), although there was no difference in paternity between polygynous and monogamous males (primary females: 16/34 (47%) of nests contained EPO, 34/104 (33%) of offspring were EPO; secondary females: 6/10 (60%) of nests contained EPO, 11/31 (35%) of offspring were EPO; all $P > 0.9$). We did not include nests of secondary females in tests of factors predicting extrapair paternity.

Colour Analysis

To avoid multicollinearity among factors in multiple regression, we examined pairwise correlations between all predictor variables. Bib size was not related to any measure of colour; however, tail brightness and tail redness (PC1) were negatively correlated ($r^2 = 0.54$, $N = 73$, $P < 0.001$). There were no relationships between any of the other predictor variables (all $P > 0.21$). Because of the correlation between tail brightness and tail redness (PC1), and the fact that tail brightness is associated with nonbreeding season territory quality in American redstarts (Reudink et al., in press), we excluded tail redness (PC1) from all regressions. However, substituting tail redness (PC1) for brightness yielded results that were qualitatively the same for all tests, except that only tail brightness (not redness (PC1)) predicted polygyny.

When we examined individuals recaptured in subsequent seasons, we found that tail feather redness (PC1) decreased with age (matched-pairs t test: $t_{17} = -2.15$, $P = 0.046$) while flank brightness increased and redness (PC1) decreased marginally, but not significantly (flank brightness: $t_{14} = -1.96$, $P = 0.07$; flank redness (PC1): $t_{15} = 1.81$, $P = 0.09$). Tail brightness and bib size did not change between year X and year $X + 1$ ($t_{18} = -0.71$, $P = 0.50$; bib size: $t_{16} = -0.39$, $P = 0.70$).

Polygyny and colour

Results of a backward stepwise nominal logistic regression with polygyny as a binary response variable (polygynous/monogamous) and tail brightness, flank brightness, flank redness (PC1), bib size, year, arrival date and body size as main effects revealed that males with brighter tail feathers were more likely to be polygynous (chi-square test: $\chi^2_1 = 6.15$, $N = 73$, $P = 0.01$; Wald test: $\chi^2_1 = 4.62$, $N = 73$, $P = 0.03$).

Paternity and colour

Stepwise nominal logistic regression with presence/absence of extrapair offspring in the nest (yes/no) and tail brightness, flank brightness, flank redness (PC1), bib size, year, arrival date and body size as main effects revealed that increased flank redness (PC1) best predicted paternity (chi-square test: $\chi^2_1 = 5.15$, $N = 41$, $P = 0.02$; Wald test: $\chi^2_1 = 4.36$, $N = 41$, $P = 0.04$). Backwards stepwise multiple regression revealed that the proportion of extrapair offspring in a males' nest was also significantly predicted by increased flank redness (PC1) ($F_{1,40} = 9.28$, $N = 41$, $P = 0.004$). None of the variables entered into a backward stepwise multiple regression significantly predicted whether males were extrapair sires.

Pairwise comparisons of within-pair males and all extrapair sires revealed that the tail and flank feathers of extrapair sires were less red than the males they cuckolded (Table 1). However, when we averaged the predictor variables of the extrapair sires in cases where there was more than one extrapair sire, only flank redness

Table 1
Plumage characteristics and arrival dates of within-pair (WP) and extrapair (EP) American redstart males at nests in which more than one male sired extrapair offspring (all EP sires) and averaged for all extrapair sires (averaged EP sires)

	Tail brightness	Tail redness (PCI)	Flank brightness	Flank redness (PCI)	Arrival date	Bib size	Body size
All EP sires							
WP male	17.55	0.4	15.32	−2.07	15.77	2.43	63.19
EP male	17.13	1.43	17.91	2.16	10.32	2.77	62.95
Mean difference	−0.42±0.55	1.83±0.81	2.59±1.39	4.22±1.54	−5.45±2.01	0.33±0.33	−0.24±0.44
df	18	18	16	17	21	20	20
t	−0.77	2.25	1.86	2.74	−2.71	1.01	−0.55
P	0.45	**0.04**	0.08	**0.01**	**0.01**	0.32	0.59
Averaged EP sires							
WP male	17.49	0.15	14.98	−1.42	14.64	2.62	63.42
EP male	17.27	1.6	17.7	2.49	9.57	2.74	63.12
Mean difference	−0.22±0.57	1.45±0.98	2.72±1.93	3.91±1.53	−5.07±2.38	0.13±0.37	−0.31±0.46
df	11	11	10	11	13	12	12
t	−0.38	1.49	1.41	2.56	−2.13	0.34	−0.66
P	0.71	0.17	0.19	**0.03**	0.053	0.74	0.52

Significant values are given in bold.

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(PC1) differed significantly between within-pair and extrapair sires, although arrival date approached significance (Table 1). Increased realized fledging success (actual within-pair offspring at both the primary and secondary nest, if polygynous, plus extrapair offspring sired in other nests) was significantly predicted by early arrival date ($F_{1,41} = 4.77$, $N = 42$, $P = 0.03$).

DISCUSSION

Our results suggest that the carotenoid-based tail and flank feathers of American redstarts may be different signals intended for different receivers. We found that redstarts with brighter tails were more likely to attain polygyny, while redstarts with more red (PC1) flanks were more likely to retain paternity at their nest (Fig. 2). Ultimately, however, realized fledging success was best predicted by arrival date on the breeding grounds. This result is consistent with previous research on our study system indicating that early arrival, driven by conditions experienced during the nonbreeding season, significantly predicts realized fledging success (Reudink et al., unpublished data).

When we examined the plumage correlates of monogamous and polygynous males, only tail brightness predicted whether individuals achieved polygyny. Because achieving polygyny is highly dependent on males securing and defending multiple territories (Secunda & Sherry 1991), our results support the idea that tail brightness may function in male–male competition and agonistic interactions. Interestingly, bib size, a trait commonly associated with dominance and male–male competition (Senar 2006), was not related to polygyny or any of the other reproductive variables we measured. This result is somewhat surprising, as Lemon et al. (1992) previously reported that males with smaller bibs had higher reproductive success (New Brunswick, Canada). Our previous work on an overwintering population of American redstarts also failed to find any evidence for bib size acting as a social signal during the nonbreeding season (Reudink et al., in press). It is possible that bib size is related to other aspects of male quality (e.g. parental care) that were not measured in this study.

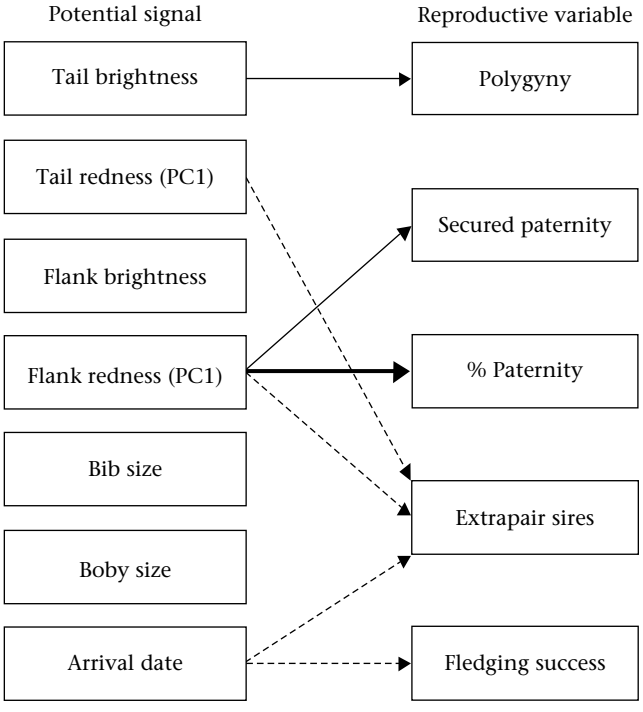

Figure 2. Relations between potential signals/predictor variables and reproductive variables. Solid lines represent significant positive relationships; dashed lines represent significant negative relationships. Thin lines represent $P < 0.05$; thick lines represent $P < 0.01$. For the reproductive variables: polygyny = whether males were polygynous or monogamous; secured offspring = whether the within-pair male sired all offspring at his nest; % paternity = the proportion of within-pair offspring that a social male sired; extrapair sires = the difference between within-pair males and the extrapair sires; fledging success = number of within-pair offspring fledged at primary and secondary (if polygynous) nests + number of extrapair offspring fledged.

Unlike attaining polygyny, securing within-pair paternity was best predicted by flank redness (PC1). Males with more red flanks were less likely to lose paternity and sired a higher proportion of their own offspring. Because within-pair paternity should be driven in large part by female choice (Andersson 1994; Hill 2006), we suggest that females may decide to pursue extrapair copulations on the basis of male flank coloration. If so, this would suggest that flank redness is acting as an intersexual signal directed towards females. Interestingly, extrapair sires, compared to the social males at each nest, arrived earlier and had significantly less red flank feathers. These results run contrary to our finding that males with more red flanks were less likely to lose paternity.

While more study is needed, the finding that males that were more red were better able to retain paternity whereas males that were less red were better able to sire extrapair offspring may reveal opposing selective pressures. For example, Delhey et al. (2003) showed that male blue tits, *Cyanistes caeruleus*, with more UV-shifted crown hue were less likely to lose paternity, whereas older males and males with less UV-shifted crown hue were more likely to sire extrapair offspring. Unlike our study, however, Delhey et al. (2003) found no difference in UV ornamentation between within-pair males and extrapair sires. The authors suggested that this could be due to a trade-off between UV ornamentation and traits that optimize extrapair success. While we do not currently have data to address this question, it is possible that our results reflect alternative mating tactics whereby males with more red flanks increase success through within-pair paternity while less ornamented males increase success through extrapair paternity.

The finding that increased flank redness (PC1) is associated with retaining paternity is consistent with our understanding of signal honesty in carotenoid-based plumage coloration, but the relationship between gaining extrapair paternity and decreased redness runs contrary to our expectations. Generally, plumage redness is associated with increased carotenoid deposition, and thus, birds with more red plumage would be assumed to be of higher quality (Saks et al. 2003a). Plumage coloration, however, is a result of multiple processes that influence a given signal and is not necessarily as straightforward as carotenoid acquisition/deposition increasing feather redness (PC1) and thus indicating individual quality. Plumage coloration is influenced both by feather structure and pigment deposition (Saks et al. 2003a; Shawkey & Hill 2005) and can also be influenced by feather abrasion (Blanco et al. 2005) and moult location or carotenoid availability (McGraw 2006). Redstart feathers contain the carotenoid pigments canary xanthophylls A and B and canthaxanthin (McGraw et al. 2005), and it remains unknown how the ratio and bulk depositions of these pigments, as well as variation in feather microstructure, contribute to the overall colour display shown by these birds. It will be informative to learn whether redness (PC1) decreases because of decreased levels of the red pigment canthaxanthin, or whether decreased redness (PC1) is actually the result of increased concentrations of the yellow pigments, canary xanthophylls A and B. Our finding that increased tail feather brightness was correlated with achieving polygyny is not surprising given that higher plumage brightness in redstarts is also correlated with higher territory quality in winter (Reudink et al., in press). In other species, plumage brightness may predict mating success (golden-collared manakin, *Manacus vitellinus*; Stein & Uy 2006) and body condition (Saks et al. 2003b).

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One explanation for why extrapair sires had less red flanks could be due to age-related changes in plumage coloration. While it is possible that low flank redness (PC1) is a direct indicator of male quality, relationships between reduced ornamentation and male success may arise if decreased redness (PC1) is correlated with male characteristics, such as male age, that are related to female choice. By examining males captured in year x and recaptured in year $x+1$, we found that tail feathers became significantly less red in year $x+1$, while flanks became marginally brighter and less red in year $x+1$. These changes appeared to be driven by increased reflectance in the UV and an associated rise in the blue-green 'trough' in year $x+1$. Thus, it is possible that the shift in plumage ornamentation, observed as a decrease in plumage redness, actually represents a change in feather microstructure and increased UV reflectance, which may be important for attracting extrapair partners (Delhey et al. 2003). In their first breeding season, males have female-like plumage and suffer highly reduced reproductive success, indicating there is a clear premium for males to acquire ASY plumage. Given that so few SY males successfully pair or raise offspring, ASY plumage, in and of itself, does not indicate that males are experienced breeders. Our results suggest that because tail and flank plumage decreases in redness (PC1) as ASY males age, plumage colour has the potential to signal male age and previous breeding experience once males acquire ASY plumage. Longitudinal studies examining individuals recaptured in multiple seasons could reveal whether patterns of paternity and polygyny co-vary with changes in plumage coloration.

With respect to the evolution of multiple ornaments in American redstarts, our finding that tail brightness predicted polygyny whereas flank redness (PC1) predicted within-pair paternity suggests that the tails and flanks of American redstarts may act as signals intended for different receivers (Pryke et al. 2001). Specifically, we suggest that tail brightness may act as an intrasexual signal functioning in territory maintenance and defence, while flank redness acts as an intersexual signal important for female mate choice decisions. Needed still are aviary-based experimental studies. It is possible that because polygyny is highly dependent on securing multiple territories, tail feather brightness may serve as a signal of competitive ability, while flank redness (PC1) functions in female choice. Furthermore, our results support the idea that tail brightness has a dual function both during the breeding and nonbreeding periods (Reudink et al., in press).

Overall, the results of our study support the idea that American redstarts display multiple plumage-based signals intended for different receivers. Furthermore, we show that a trait implicated as an agonistic signal during the nonbreeding period (Reudink et al., in press) may also serve to enhance reproductive success on the breeding grounds. Tail feather brightness appears to function as an intrasexual signal, both during the breeding and nonbreeding seasons, while flank redness (PC1) appears to be important for intersexual signalling. A potential, but as yet untested, hypothesis is that because tail brightness appears to signal an individual's ability to obtain a high-quality territory during the nonbreeding season, individuals may use that information, obtained thousands of miles from the breeding grounds, to inform mate choice decisions and to inform the decision to engage in agonistic interactions. If so, this would suggest that an apparent agonistic signal used during the nonbreeding season in the tropics can carry-over to influence breeding season dynamics, a pattern thus far only observed in temperate residents (e.g. Mennill et al. 2003; Doucet et al. 2005).

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