ADULT-LIKE PLUMAGE COLORATION PREDICTS WINTER TERRITORY QUALITY AND TIMING OF ARRIVAL ON THE BREEDING GROUNDS OF YEARLING MALE AMERICAN REDSTARTS

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Abstract. The quality of winter territory can have important consequences for migratory songbirds throughout the year. In the American Redstart (*Setophaga ruticilla*), a warbler in which plumage maturation is delayed, yearling males winter in a variety of habitat types that vary in quality. Little is known regarding which physical traits allow some yearlings to occupy higher-quality sites. Here, we measured eight variables characterizing the plumage and morphology of yearling males in two habitats that differ in suitability to determine which aspects of phenotype predict winter habitat occupancy. Yearlings wintering in high-quality mangrove habitat in Jamaica had more extensive adult-like black plumage on their breast than those in low-quality scrub. No other phenotypic differences associated with winter habitat were detected. Additionally, yearling males arriving earlier on the breeding grounds in Ontario had more extensively black breasts than those arriving later. Previous studies using stable carbon isotopes have linked adult male American Redstarts' date of arrival in the breeding range with quality of their winter habitat. Our findings indicate an association between the extent of adult-like plumage and habitat occupancy, suggesting that variation in yearling males' appearance may be correlated with their ability to compete for high-quality habitat.

Key words: American Redstart, arrival date, delayed plumage maturation, plumage color, Setophaga ruticilla, *winter habitat quality, yearling plumage.*

La Coloración de Tipo Adulto Predice la Calidad de los Territorios de Invernada y el Tiempo de Llegada a las Áreas Reproductivas de Individuos de un Año de *Setophaga ruticilla*

Resumen. La calidad de los territorios de invernada puede tener consecuencias importantes para las aves a través de todo el año. *Setophaga ruticilla* es una especie de ave que alcanza la madurez del plumaje en forma tardía y cuyos machos de un año pasan el invierno en una variedad de hábitats que difieren en calidad. Se sabe poco sobre cuáles características físicas son las que permiten a algunos individuos de un año ocupar los sitios de mayor calidad. Para predecir cuales aspectos del fenotipo predicen la ocupación de sitios en las áreas de invernada, medimos ocho variables que caracterizan el plumaje y la morfología de los machos de hasta un año, en dos hábitats que difieren en calidad. Los individuos que ocuparon hábitats de manglar de alta calidad en las áreas de invernada en Jamaica tuvieron un plumaje negro tipo adulto más desarrollado en el pecho que aquellos individuos que ocuparon áreas arbustivas de baja calidad. No se detectaron otras diferencias fenotípicas asociadas a los hábitats de invernada. Además, los machos de hasta un año que llegaron más temprano a las áreas de reproducción en Ontario tuvieron pechos de color negro más desarrollado que aquellos que llegaron más tarde. Estudios anteriores que utilizaron isótopos estables han relacionado la fecha de llegada a las áreas de reproducción con la calidad de sus hábitats de invernada. Nuestros resultados indican una asociación entre el grado de desarrollo del plumaje tipo adulto y la ocupación de hábitat, lo que sugiere que la variación en la apariencia de individuos de hasta un año puede estar correlacionada con su capacidad de competir.

INTRODUCTION

The quality of winter habitat plays an important role in the life history of many species of migratory birds. For some warblers wintering in the neotropics, such as the American Redstart (*Setophaga ruticilla*), competition in the nonbreeding season leads to habitat occupancy biased by age and sex, with adult males occupying the majority of high-quality winter territories (Marra et al. 1993, Marra 2000). American Redstarts wintering in high-quality habitat such as coastal mangrove forests have access to abundant and reliable food supplies throughout the winter (Studds and Marra 2005, 2007). As a consequence,

these birds are in better condition and their annual survival is higher than that of those wintering in low-quality scrub habitat (Marra et al. 1998, Marra and Holberton 1998, Marra and Holmes 2001). The carry-over effects of winter habitat quality into the breeding season represent subsequent additional advantages associated with occupying superior habitats. Adult male American Redstarts wintering in high-quality territories begin spring migration earlier, arrive on the breeding grounds earlier, and realize greater reproductive success than those from low-quality territories (Marra et al. 1998, Reudink et al. 2009a). Recent evidence suggests that winter habitat occupancy during an individual's first year also plays an important role in natal dispersal, indicating that yearlings' acquisition of winter habitat may influence the American Redstart's distribution (Studds et al. 2008).

Previous work on wintering American Redstarts has demonstrated that females experience size-based habitat segregation, with larger females outcompeting smaller females for territories in mangrove habitat. Males' body size is not related to their winter habitat (Marra 2000, Reudink et al. 2009b). Instead, their ability to compete may be associated with carotenoid-based plumage features, with both yearling and adult males in high-quality habitat having brighter tail feathers (Reudink et al. 2009b). Although these results suggest yearling male American Redstarts may use carotenoid-based plumage signals in winter territorial interactions, no study has incorporated quantitative measures of black (melanin-based) plumage patches of young males or controlled for possible age-related differences in the size of patches of carotenoid plumage. Little else is known about what factors influence the ability of yearling males to occupy territories in habitat typically dominated by adult males.

American Redstarts undergo delayed plumage maturation (DPM); adult males are distinguished by their glossy black coloration, with orange patches on their wings, tail, and flanks (Sherry and Holmes 1997). Females and yearling males are primarily olive-gray, with yellow patches on the wings, tail, and flanks. The orange patches on adults' tail feathers are significantly larger than the yellow patches of yearling males (R. Germain, unpubl. data). However, yearling males may also exhibit some orange coloration similar to that of adult males, as well as irregular black patches, primarily on the head and breast (Sherry and Holmes 1997). The extent of this black varies greatly from bird to bird, and black feathers grow in as a result of adventitious feather loss starting in August of the natal year until the molt into definitive plumage at the end of the first breeding season (Rohwer et al. 1983, Sherry and Holmes 1997). Although Rohwer et al. (1983) suggested that the growth of such black plumage around the eyes may be related to increased foraging efficiency during winter, the advantages/disadvantages for yearling males of possessing more or less black plumage during either the breeding season or winter has been little investigated.

Classic studies of songbird species with DPM considered immature plumage to be an adaptation to the first winter (Rohwer et al. 1983, Rohwer and Butcher 1988). However, the selective advantages of DPM for wintering yearling songbirds are still ambiguous and may differ by species (Cucco and Malacarne 2000, Karubian et al. 2008). Although other theories predict that the advantages of DPM may be manifested during the first breeding season, unambiguous benefits of DPM as either a breeding- or nonbreeding-season adaptation have yet to be indentified (Cucco and Malacarne 2000, Froehlich et al. 2004). Alternatively, DPM may be the result of physiological constraints on molt, subordinate yearling males being unable to compete for resources and incapable of growing showy adult feathers during their partial molt before fall migration (Rohwer 1983, 1986, Rohwer and Butcher 1988). When feathers are lost adventitiously, however, newly grown feathers appear more adult-like than those they replace (Rohwer et al. 1983, Rohwer and Butcher 1988). Although the basis and extent of adventitious feather loss is highly variable, one potential cause is territorial battles, in which competing males may peck and grapple, tearing out feathers during physical encounters (e.g., Belthoff and Gauthreaux 1991, Stutchbury 1991). Variation among yearling males in the extent of patches of adult-like plumage could function as a signal of fighting experience, indicating a yearling's chances of defending a resource such as high-quality winter habitat. Tests of these hypotheses have languished because of the lack of studies measuring individual plumage variation in yearling males in species with DPM and investigating how plumage functions in winter territorial signaling (Froehlich et al. 2004).

In this correlative study, we quantify several aspects of plumage ornamentation and body size of yearling male American Redstarts, and we link individual variation in overall appearance with winter habitat type. We use two approaches: capturing yearling males on their respective winter territories in Jamaica and during their first breeding season in Ontario and inferring the quality of their previous winter habitat from signatures of stable carbon isotopes in tissue samples. This study extends that of Reudink et al. (2009b) by asking whether in acquiring winter territories yearling males use plumage signals additional to or different from those of adult males, and by measuring additional characteristics of yearling males' plumage not considered in previous studies to better characterize variation in yearling males' overall appearance. If yearling males with more adult-like features are able to secure and defend high-quality winter territories, it would suggest that variation in yearlings' appearance may signal individual status and competitive ability.

METHODS

FIELD DATA

Our field work during the nonbreeding season took place in high-quality (black mangrove, *Avicennia germinans*) and low-quality (second-growth scrub) habitats at Font Hill Nature

Preserve, Westmoreland Parish, Jamaica, West Indies (18° 02′ N, 77° 57′ W), during a period when wintering American Redstarts are stationary (22 October–18 November 2008). This period corresponds to the time shortly after the redstarts establish their winter territories, allowing us to investigate potential correlations between phenotype and territory establishment. During the breeding season (1 May–20 July 2008), our study site was the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44° 34′ N, 76° 19′ W). American Redstarts begin to arrive on their wintering grounds from mid-to-late September through October, and they remain territorial through the entire nonbreeding period (Holmes et al. 1989, Marra 2000). In Jamaica, the early part of the redstart's wintering season is typically more mesic than later winter (Studds and Marra 2005). In Ontario, we surveyed daily to determine the arrival date of all males. We then ranked the birds' arrival, to account for missing data ($n = 9$) where the order in which the individual arrived was known but the precise date (within a 2- to 3-day window) was not. In instances of a tie in two individuals' arrival date or inferred arrival date ($n = 4$), we assigned arrival order by flipping a coin.

On both the breeding and wintering grounds, we captured yearling male American Redstarts with mist nets on their respective territories (determined via daily surveys both before and after the day of capture), using a combination of both passive netting and song playbacks accompanied by a decoy. We aged and sexed all captured birds (Jamaica: $n = 17$, Ontario: $n = 22$) according to Pyle (1997) and banded them with a unique combination of two or three color bands and either a U.S. Fish and Wildlife Service (Jamaica) or Canadian Wildlife Service (Canada) aluminum band. From each captured bird, we recorded the wing chord (mm), mass (g), tarsus length (mm), and tail length (mm). For plumage analysis, we plucked a single tail feather (rectrix 3), and took four or five pictures (Canon Powershot A460) of each individual in a series of standard poses in front of a gridded background. From males captured in Ontario, we also collected 2–3 mm of tissue from the central claw of each foot for use in analysis of stable carbon isotopes.

PLUMAGE ANALYSIS

We uploaded standardized photos into Adobe Photoshop CS3 (v. 10.0) at a resolution of 2592 × 1944 pixels, then measured the area of black (adult-like) plumage on both the head (from behind bill to nape, including lores, hereafter called head) and breast (chin, throat, and breast, hereafter called breast). We named the image files by the individual's band number, and no information regarding habitat type was available at the time of measurement. We selected the black regions with the "lasso" tool, and determined the number of pixels occupied by black plumage with the histogram palette. Using one of several standard grid squares (area 37.58 mm^2) in each photo, we calculated the total area (mm^2) of black plumage visible for each region.

In this population, wing length has been used consistently as the standard measure of body size (Reudink et al. 2009b, c). We used wing length to standardize the size of black plumage patches (dividing the area of black plumage in each region by wing length) and in all subsequent measures of body size.

We quantified the extent of patches of color in the rectrices plucked from yearlings' tails by measuring the area (mm^2) of carotenoid-based yellow patches on both sides of the rachis with digital calipers (±0.01 mm). We then divided this measure by the total area of the tail feather, to control for feather size.

Following Reudink et al. (2009b), we mounted the plucked rectrices on low- (<5%) reflectance paper, and we recorded reflectance spectra with an Ocean Optics USB4000 spectrometer (Dunedin, FL) attached to a PX-2 pulsed xenon light source. If the patch of color was too small to yield accurate reflectance readings (Jamaica: $n = 4$, Ontario: $n = 4$), we excluded reflectance spectra of that patch from further analysis. We took 25 measures throughout the yellow region of each tail feather and calculated standard measures of brightness, hue, and chroma (saturation) by the following equations:

$$\text{Brightness} = R_{\lambda 320-700}/n$$
$$\text{Hue} = \arctan\{[(R_{\lambda 510-605} - R_{\lambda 320-415})/R_{\lambda 320-700}]/[(R_{\lambda 605-700} - R_{\lambda 415-510})/R_{\lambda 320-700}]\}$$
$$\text{UV chroma} = R_{\lambda 320-415}/R_{\lambda 320-700}$$
$$\text{Red chroma} = R_{\lambda 575-700}/R_{\lambda 320-700}$$

where $\lambda a{-}b$ represents the light reflected at each wavelength from a through b (measured in 1-nm bins) and n equals the number of 1-nm bins from a through b (Montgomerie 2006a).

ANALYSIS OF STABLE CARBON ISOTOPES

Signatures of stable carbon isotopes (δ^{13}C) in plants vary across different tropical habitat types because of differences in water stress and photosynthetic system (Lajtha and Marshall 1994). These signatures are transferred up the food chain (plant to insect, insect to insectivore) and eventually become incorporated into bird tissue. The quality of an American Redstart's winter territory can then be inferred from the δ^{13}C signature of sampled tissue, where more negative values of δ^{13}C indicate more mesic winter habitats (Marra et al. 1998).

Stable carbon isotopes in collected claw tissue were analyzed at the Queen's University Facility for Isotope Research (Kingston, ON) as by Reudink et al. (2009a, b).

STATISTICAL ANALYSIS

All analyses were done with JMP 8.0.1 (SAS Institute 2009) and R 2.10.1 for Windows (R Development Core Team 2009). We tested all variables for assumptions of normality (Shapiro–Wilks test) and equal variance (Levene's homogeneity of variance test). All variables except the areas of black plumage on the head and breast were normally distributed. We transformed both variables by taking the square root of each measure for

all individuals on both the breeding and wintering grounds. We then tested the morphological and plumage variables from birds captured in Jamaica for multicollinearity with Pearson's correlational analysis and for outliers with Mahalanobis distance-outlier analysis. Pearson's analysis revealed significant co-linearity ($r > 0.7$: McGarigal et al. 2000) between the following pairs of variables: red chroma and UV chroma, red chroma and hue, and tail patch size and tail brightness. For these collinear variables, we calculated univariate ANOVAs (with habitat as the fixed factor) and compared their F-values, retaining variables with the highest F-value while excluding those with lower F-values from discriminant analysis (Noon 1981, Herring et al. 2008). We then entered measures that met all criteria (area of black breast plumage, area of black head plumage, wing length, size of tail patch, and red chroma of tail) into a discriminant function analysis (DFA) to determine the best single variable or combination of variables that separated yearling male American Redstarts by habitat. In addition, we compared all plumage variables, as well as morphology, across habitat type with one-way ANOVAs. For birds captured in Ontario, we used a series of linear regressions to compare the same measures of plumage coloration and morphology with arrival rank. Finally, we compared arrival rank and the extent of black head and breast plumage with signatures of stable carbon isotopes from collected claw tissue with linear regressions and included post-hoc power analyses to account for small sizes of isotopic samples.

RESULTS

Discriminant function analysis significantly separated yearling males by nonbreeding habitat type; canonical variate scores of males in mangrove habitat were higher than scores of those in scrub (two-tailed t-test with equal variance: $r^2 = 0.72$, $t_{11} = -5.30$, $P = 0.0003$; Fig. 1). Discriminant function analysis predicted winter habitat occupancy with 92% accuracy (8/8 birds
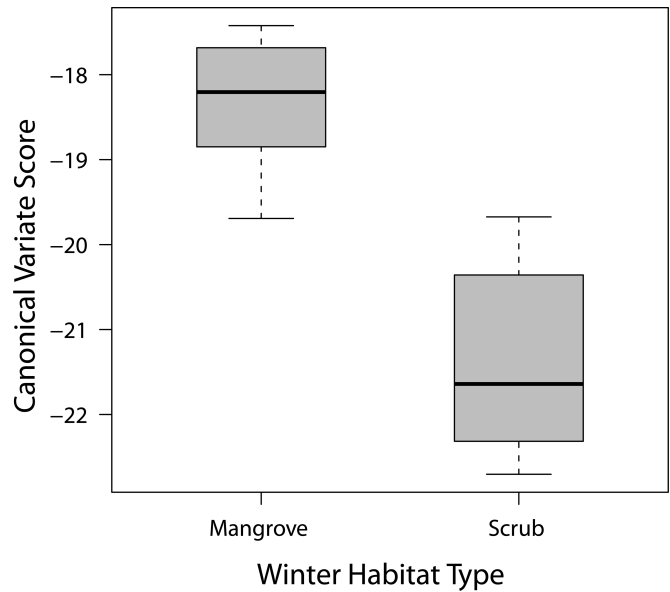

FIGURE 1. Box plot of canonical variate scores of the plumage of yearling male American Redstarts wintering in mangrove ($n = 8$), and scrub ($n = 5$) habitat. Horizontal lines represent the median, 25th, and 75th percentiles and maximum and minimum values, respectively.

found in mangrove and 4/5 found in scrub). Canonical scores were significantly positively correlated with black breast plumage ($r^2 = 0.68$, $F_{12} = 23.62$, $P = 0.0005$), mangrove males having more extensively black breasts. Wintering in mangroves was also associated positively (but not significantly) with both extent of black on the head ($r^2 = 0.24$, $F_{12} = 3.43$, $P = 0.09$) and size of the tail patch ($r^2 = 0.21$, $F_{12} = 2.85$, $P = 0.12$). One-way ANOVA with habitat type as the predictor variable also found that yearling males in mangrove had significantly more black breast plumage than those in scrub (Table 1). In addition, mangrove birds appeared to have more black head plumage and

TABLE 1. Results of one-way ANOVAs comparing variances of wing length and plumage variables (mean ± SD) of yearling male American Redstarts wintering in either high-quality mangrove ($n = 11$) or low-quality scrub ($n = 6$) habitat. Area of black breast and black head plumage (mm^2) are controlled for body size (wing length). Degrees of freedom for a variable change where data from individuals were missing.

Variable	Mangrove	Scrub	R^2	F	P	Power
Wing length (mm)	61.0 ± 1.3	62.3 ± 1.4	0.20	3.67[a]	0.08	0.43
Black head plumage	0.27 ± 0.19	0.15 ± 0.20	0.20	3.83[a]	0.07	0.45
Black breast plumage	0.55 ± 0.18	0.18 ± 0.17	0.52	16.18[a]	**0.001**	0.96
Tail patch size (mm^2)	0.49 ± 0.18	0.26 ± 0.31	0.02	0.23[b]	0.63	0.07
Tail brightness	19.01 ± 2.18	18.83 ± 2.02	0.002	0.02[c]	0.88	0.05
Tail UV chroma	0.24 ± 0.004	0.24 ± 0.006	0.11	1.32[c]	0.27	0.18
Tail red chroma	0.39 ± 0.005	0.39 ± 0.01	0.02	0.18[c]	0.68	0.08
Tail hue	0.32 ± 0.04	0.34 ± 0.05	0.04	0.40[c]	0.54	0.09

[a] df = 1,15.
[b] df = 1,14.
[c] df = 1,11.
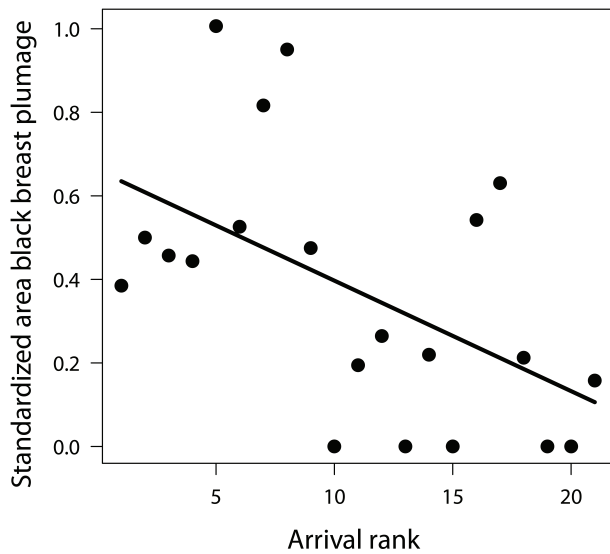
FIGURE 2.   Linear regression of rank of arrival of yearling male American Redstarts on the breeding grounds and area (mm^2) of their black breast plumage, standardized by wing length.

smaller body size, although neither relationship was significant (Table 1). No other variables differed significantly by habitat (all $P > 0.27$).

Arrival rank of yearling males captured on the breeding grounds in Ontario was negatively correlated with the area of black breast plumage ($r^2 = 0.28$, $F_{1,19} = 7.39$, $P = 0.01$; Fig. 2), early-arriving males having more extensively black breasts. There were no relationships between arrival rank and wing length, black head plumage, or any measure of rectrix coloration (all $P > 0.12$).

Signatures of stable carbon isotopes ($\delta^{13}C$) in claws were not significantly correlated with arrival rank, although statistical power was low (Table 2). Values of $\delta^{13}C$ in claw tissue were likewise not significantly correlated with the area of black breast plumage (Table 2). However, the association ($P = 0.06$; Table 2) between $\delta^{13}C$ signatures and black head plumage was negative, the birds with more extensive adult-like plumage on

TABLE 2.   Results of linear regression analysis between signatures of stable carbon isotopes ($\delta^{13}C$) in claw tissue collected during the breeding season and arrival rank, morphology, and plumage coloration of yearling male American Redstarts. Area of black breast and black head plumage (mm^2) are controlled for body size (wing length).

Variable	R^2	F	P	Power
Arrival rank	0.008	0.08[a]	0.79	0.05
Black head plumage	0.37	4.61[b]	0.06	0.47
Black breast plumage	0.15	1.35[b]	0.28	0.18

[a]df = 1,9.
[b]df = 1,8.

their heads tending to have tissue signatures consistent with high-quality wet winter habitat.

DISCUSSION

Yearling male American Redstarts captured in high-quality mangrove habitat had more extensive black adult-like plumage on their breast than those in low-quality scrub. Yearling males that arrived on the breeding grounds earlier similarly expressed more adult-like breast plumage than did males arriving later. Although these results are based on a small sample collected within a single year, the significant relationship of black plumage during both the nonbreeding and breeding seasons suggests that variation in yearling males' appearance may be associated with a young male's ability to occupy superior territories through the winter and depart earlier for the breeding grounds.

Although yearling males arriving in the breeding range earlier had more extensively black breasts than those arriving later, we found no significant relationships between winter habitat quality (inferred by analysis of stable carbon isotopes) and either arrival or plumage coloration. These findings contrast with the significant relationships between winter habitat and both arrival (Reudink et al. 2009a) and one plumage character (brightness) (Reudink et al. 2009b) found in adult males. Although the directionality of $\delta^{13}C$ signatures of claws and black plumage on the head and breast was consistent with our other findings (Table 2), the sample size used in the carbon-isotope analysis may have been insufficient to detect any biologically meaningful relationships, and further sampling is required before any conclusions can be drawn from these results.

Further studies using larger sample sizes and territory-intrusion experiments are also needed to determine if yearling males with more adult-like appearance are more aggressive in territorial interactions in winter. In the American Redstart, the extent of young males' black plumage tends to increase through the year (Rohwer et al. 1983). Therefore, longitudinal studies involving repeated measures of marked individuals are necessary to ensure that the relationship between the extent of black plumage and territory quality persists as conditions become drier throughout the winter months and birds begin preparing for spring migration.

In Jamaica, discriminant function analysis revealed that while multiple predictors contributed to the habitat-based separation of yearlings based on overall appearance, only the area of black breast plumage was statistically significant. When all plumage and morphologic variables were analyzed separately, again only black breast plumage differed significantly by habitat type. Reudink et al. (2009b), studying the American Redstart's plumage coloration on the wintering grounds, found that tail brightness differed by habitat type, regardless of age class. Although this previous study included a larger sample of yearling males, Reudink et al. (2009b) did not incorporate measures of adult-like black plumage or the extent of the patch

of color in the tail in their analysis. Although we did not find tail-patch size in the two habitats we study to differ significantly, the positive association between patch size and canonical variate score in this small sample warrants consideration. In both the present study and a larger dataset of males in Ontario (R. Germain, unpubl. data), tail brightness and tail-patch size are positively correlated in yearling males. Therefore results of yearlings' tail coloration should be interpreted cautiously; the mean size of yearlings' patches is significantly smaller than that of adults. In addition, differences between shaded mangrove sites and exposed scrub sites in exposure to UV radiation could result in different rates of feather wear and color degradation (Montgomerie 2006b, Surmacki 2008). Because field work for our study took place early during the period of the redstart's wintering (October–November rather than December–March in Reudink et al. 2009b), we are less likely to have observed differences in plumage coloration that could be attributed to environmental effects differing by habitat. In our study, the body size of yearling males in mangrove and scrub habitat did not differ significantly, although there was a trend toward birds captured in mangrove having shorter wing chords. Several previous studies using larger samples at the same field site have likewise found no differences by habitat in the body size of yearling or adult males (Marra 2000, Reudink et al. 2009b). In addition, no other measures of yearling males' body size appear to differ by habitat (e.g., mass, tarsus and tail length; R. Germain, unpublished data).

Yearling males occupying high-quality winter territories and those arriving earlier on the breeding grounds had more extensive black plumage, consistent with the theory that the size of melanin-based plumage badges is commonly associated with dominance and competition between males (Senar 2006). Because in the winter range American Redstart feathers are grown adventitiously, more extensive black body plumage may signal an individual's tendency to defend its territory against intruders, black feathers arising as a result of feather loss in territorial fights. Feather loss during fights is common in small migratory birds such as the Purple Martin (*Progne subis*; Stutchbury 1991), and male American Redstarts in mangrove habitat are known to act more aggressively toward territorial intruders than those in scrub (Marra 2000). Alternatively, recent evidence suggests that the size of melanin-based plumage patches may be under hormonal control (reviewed by McGraw 2006) or affected by the diet's calcium content, indicating that black plumage may be condition dependent (McGraw 2007). Although the mechanism responsible for the greater extent of black plumage in yearling males overwintering in mangrove habitat is unknown, ours is the first study to explore variation in the appearance of yearling males with DPM across nonbreeding-season habitats that vary in quality. Our findings are consistent with the theory that yearlings may use adult-like plumage to advertise their quality, and our results suggest that yearling males with more extensive patches of adult-like plumage can compete successfully with adults for high-quality resources and that variation in subadult males' plumage may act as a status signal during the nonbreeding season.

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